ZooKeys 1208: 1–48 (2024)
DOI: 10.3897/zookeys.1208.122829

Research Article

Revision of the Oriental species of the hoverfly genus *Paramixogaster* Brunetti, 1923 (Diptera, Syrphidae, Microdontinae)

Menno Reemer[1], Hariharakrishnan Sankararaman[2]

1 Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, Netherlands
2 Department of Crop Protection (Entomology), Vanavarayar Institute of Agriculture, Manakkadavu, Pollachi, Coimbatore, Tamil Nadu 642103, India
Corresponding author: Menno Reemer (menno.reemer@naturalis.nl)

Abstract

The species of the hoverfly genus *Paramixogaster* Brunetti, 1923 from the Oriental Region are revised. The resulting number of valid species is 15, of which the following four are described as new: *P. halmaherensis* Reemer, **sp. nov.**, *P. jubata* Reemer, **sp. nov.**, *P. kodaiana* Sankararaman & Reemer, **sp. nov.**, and *P. sulawesiana* Reemer, **sp. nov.** Three new synonymies are established: *Paramicrodon decipiens* de Meijere, 1917, **syn. nov.** is a junior synonym of *Microdon vespiformis* de Meijere, 1908; *Paramixogaster wegneri* Keiser, 1964, **syn. nov.** is a junior synonym of *Ceratophya indica* Doleschall, 1857; *Microdon subpetiolatus* Thompson, 2020, **syn. nov.** is a junior synonym of *Microdon contractus* Brunetti, 1923. *Paramixogaster huoi* Reemer, **nom. nov.** is introduced as a replacement name for *P. trifasciatus* Huo & Zhao, 2022, which is a primary homonym of *P. trifasciatus* Ssymank & Reemer, 2016. Neotypes are designated for *Paramixogaster icariiformis* Pendlebury, 1927 and *Myxogaster variegata* Sack, 1922, and a lectotype is designated for *Microdon vespiformis* de Meijere, 1908. An identification key to the species and diagnoses for all species are provided.

Key words: Ant flies, identification key, Indomalayan realm, morphology, new species, new synonyms, taxonomy

Academic editor: Ximo Mengual
Received: 11 March 2024
Accepted: 29 May 2024
Published: 25 July 2024

ZooBank: https://zoobank.org/5F3E1286-D578-4F4B-AD83-F5BC46D651A4

Citation: Reemer M, Sankararaman H (2024) Revision of the Oriental species of the hoverfly genus *Paramixogaster* Brunetti, 1923 (Diptera, Syrphidae, Microdontinae). ZooKeys 1208: 1–48. https://doi.org/10.3897/zookeys.1208.122829

Introduction

Hoverflies of the genus *Paramixogaster* Brunetti, 1923 are slender wasp mimics, with a more or less constricted abdomen and long antennae (Figs 1–3). They are found in the Afrotropical, Oriental, and Australasian Regions (Reemer and Ståhls 2013a). Like most other Microdontinae, but unlike most other Syrphidae, flies of this genus are not known to visit flowers (Reemer 2012). Larvae of most species are unknown, but records of a few African and Australasian species have been found in nests of ants belonging to the subfamilies Formicinae and Myrmicinae (Hymenoptera: Formicidae) (Reemer 2013). A larva of the Oriental species *Paramixogaster vespiformis* (de Meijere, 1908) was found in association with a species of the subfamily Dolichoderinae (Fig. 4; see species account of *P. vespiformis*).

Figures 1–3. Hoverflies of the genus *Paramixogaster* are slender wasp mimics, with a more or less constricted abdomen and long antennae. This male of an undescribed species was photographed in Terengganu, Malaysia, on 26 June 2021. This specimen is very similar to *P. huoi* Reemer, nom. nov. and *P. sulawesiana* Reemer, sp. nov., from which it differs by the medially interrupted fascia of golden setulae along the transverse suture on the scutum (continuous in the other two species), as well as by the dark hind legs (yellowish in the other two species). It is also similar to *P. kodaiana* sp. nov., but differs in the less extensive infuscation of the wings and the medially interrupted golden fascia along the posterior margin of the scutum (continuous in *P. kodaiana* Sankararaman & Reemer, sp. nov.). No collected specimens of this species are known, which is why it is not described in this paper. Photographs by Husni Che Ngah.

Figure 4. Larva of *Paramixogaster vespiformis* (de Meijere), attended by ants, putatively of *Dolichoderus thoracicus* (Smith). Found in Thailand and reared to the adult stage by Greg R. Ballmer. For further details, see species account of *P. vespiformis*. Photograph by G.R. Ballmer.

Paramixogaster was erected by Brunetti (1923) after he recognised that *Mixogaster vespiformis* Brunetti, 1913, a species he described from India ten years earlier, did not fit well into the New World genus *Mixogaster* Macquart, 1842. During the 20th century, only two more species were included in *Paramixogaster*: *P. icariiformis* Pendlebury, 1927 from Peninsular Malaysia and *P. wegneri* Keiser, 1964 from Ambon (Indonesia, Moluccas). The latter species has been included in species catalogues of both the Oriental and the Australasian Region (Knutson et al. 1975; Thompson and Vockeroth 1989).

When Cheng and Thompson (2008) argued that *Paramixogasteroides* Shiraki, 1930 and *Tanaopicera* Hull, 1945 should be considered synonymous with *Paramixogaster*, the type species of both genus group names were also included in *Paramixogaster*: the Oriental *Myxogaster variegata* Sack, 1922 and the Australian *Ceratophya variegata* Walker, 1852, respectively. Huang and Cheng (2012) described two *Paramixogaster* species from southern China. So, by that time, seven species were included in *Paramixogaster*, i.e., five from the Oriental Region and two from the Australasian Region, namely *P. variegatus* (Walker) from Australia and *P. wegneri* from Ambon.

The concept of *Paramixogaster* as a genus was renewed by Reemer and Ståhls (2013a, b), based on the analysis of morphological and molecular characters. They included 26 species in the genus, most of which were placed in other genera during the 19th and 20th century. According to the classification of Reemer and Ståhls (2013a), the genus is distributed not only in the Oriental and Australasian Regions, but also in the Afrotropical Region.

Since the introduction of the new generic concept by Reemer and Ståhls (2013a, b), two additional *Paramixogaster* species were described: *P. trifasciatus* Ssymank & Reemer, 2016 from Central African Republic and *P. trifasciatus* Huo & Zhao in Zhao & Huo, 2022 from China. The latter is a primary homonym of the former and we provide a replacement name in this work.

This paper revises the Oriental species of *Paramixogaster*. Before starting this revision, 13 Oriental species were included in this genus (Reemer and Ståhls 2013a; Zhao et al. 2022). These species are revised here, introducing new synonymies as well as new species, resulting in 15 Oriental species in the genus.

Materials and methods

Morphological terminology largely follows Cumming and Wood (2017) (for wing venation the 'traditional' system is used), supplemented with some terms specifically introduced for Microdontinae by Reemer and Ståhls (2013b).

Type material of previously described species has been studied when available to us. The types of *Paramixogaster icariiformis* Pendlebury, 1927, *P. fujianensis* Cheng, 2012, and *P. yunnanensis* Cheng, 2012 could not be studied (for details see species accounts). For these species, we had to rely on the original descriptions.

For studied primary types, text on labels is given ad verbatim. Text is indicated in quotation marks (" ") and each line on the label is separated by a double forward slash (//). Text not given on labels (i.e., remarks by authors) is given in square brackets ([]).

Collections are indicated by the following acronyms:

CASB	Chinese Academy of Sciences, Beijing (China)
DEI	Senckenberg Deutsches Entomologisches Institut, Müncheberg (Germany)
NHMUK	Natural History Museum, London (United Kingdom)
NMB	Naturhistorisches Museum Basel, Basel (Switzerland)
NBAIR	National Bureau of Agricultural Insect Resources, Bengaluru (India)
QSBG	Queen Sirikit Botanical Gardens, Chiang Mai (Thailand)
RMNH	Naturalis Biodiversity Center, Leiden (the Netherlands)
SUHC	Shaanxi University of Technology, Hanzhong (China)
UCRC	University of California, Dep. of Entomology, Riverside (USA)
USNM	United States National Museum, Smithsonian Institution, Washington D.C. (USA)

ZMHU	Museum für Naturkunde, Berlin (Germany)
ZMUC	Natural History Museum of Denmark, Copenhagen (Denmark)
ZSI	Zoological Survey of India, Calcutta (India)

Photographs have been made over the course of 15 years using various types of equipment across a range of circumstances in a number of different institutions, the details of which could no longer be retrieved.

Taxonomic account

Paramixogaster Brunetti, 1923

Generic diagnosis. Among Microdontinae, *Paramixogaster* is one of two microdontine genera which combines a bare postpronotum with a constricted abdomen. The only other genus to which this combination of characters applies is the Neotropical genus *Ceriomicrodon* Hull, 1937. This taxon differs from *Paramixogaster* in the widely rounded postero-apical corner of wing cell r_{4+5} (angular in *Paramixogaster*), and in the long and whip-like dorsal process of the phallus (short and as long as ventral process in *Paramixogaster*).

In two African species, the abdomen is not clearly constricted in dorsal view, but tergite 2 is dorsoventrally flattened, making the abdomen appear constricted in lateral view (Reemer and Ståhls 2013a). There are no such species known from the Oriental Region.

Nomenclatural note. As stated by ICZN article 30.1.2, names ending in -*gaster* are feminine, so the genus name *Paramixogaster* will be treated as such in this paper. Thus, conventional Latin adjectives are treated as adjectives by default under the Code (1999, Article 31.2). Nevertheless, nouns do not need to agree in gender with the generic name (ICZN, 1999, Article 31.2.1) and species-group names that can be regarded as a noun or as an adjective, when the author did not indicate how to treat them, are treated as a noun in apposition and the original spelling is to be retained (ICZN 1999, Article 31.2.2).

Key to Oriental species of *Paramixogaster*

Note that several of the included species are known from one sex only, so sexual dimorphism is unknown for these species. In general, it seems that *Paramixogaster* females tend to have a shorter postpedicel than males, as well as a larger body size. As in many other Syrphidae, females also differ from males in a wider face and abdomen. Also note that the type specimens of *P. fujianensis* and *P. yunnanensis* have not been examined, so their placement in this key is based on the descriptions and therefore should be considered tentative.

1 Postpronotum bare, abdomen constricted basally. Postero-apical corner of wing cell r4+5 angular ....**2 (*Paramixogaster*)**

– Other combination of characters .... other Microdontinae genera

2 Frons not clearly swollen, without lateral bulges (Fig. 5) **10**

– Frons swollen, with pair of lateral bulges, with narrow sulcus in between (Fig. 6) **3**

3 Tergite 2 > 2× as long as wide (Huang and Cheng 2012: fig. 415).............. ....***P. fujianensis* Cheng**

– Tergite 2 < 2× as long as wide (Figs 17, 18, 23, 99) **4**

4 Mesoscutum without golden setulae along transverse suture, at most with a small patch of golden setulae laterally at notopleuron (Fig. 7).......**8**

– Mesoscutum with fascia of golden setulae along transverse suture, either continuous or medially interrupted (Fig. 8) **5**

5 Tergite 2 with lateral margins strongly and abruptly curved upward posteriorly, giving it a saddle-like appearance (Fig. 9). Tergites 3 and 4 without fasciae of golden setulae along posterior margins (Fig. 68) ....***P. icariiformis* Pendlebury**

– Tergite 2 with lateral margins only slightly and evenly curved upward posteriorly (Fig. 10). Tergites 3 and 4 with wide fasciae of dense golden setulae along posterior margins (Figs 60, 81, 102)...**6**

6 Fascia of golden setulae along transverse suture on scutum medially interrupted (Fig. 86). Wing clearly infuscate in anterior cells, with dark colouration extending into wing cell R4+5 (Fig. 87). Tergites 3 and 4 with short black setulae over most of their surface (except for the golden posterior fasciae) ....***P. kodaiana* Sankararaman & Reemer, sp. nov.**[*]

– Fascia of golden setulae along transverse suture on scutum continuous (Fig. 60). Wing slightly brownish in anterior cells, but less clearly and dark colouration not extending into cell R4+5 (Figs 66, 106). Tergites 3 and 4 with pale (yellowish, with golden intermixed) setulae over most of their surface (except for the golden posterior fasciae)......................................**7**

7 Apex of vein R2+3 at approximately same level as joint M1 with R4+5 (Fig. 11). Face entirely yellow (Fig. 63) ....***P. huoi* Reemer, nom. nov.**

– Apex of vein R2+3 more distal than joint of M1 with R4+5 (Fig. 12). Face dark medially (Fig. 105) ....***P. sulawesiana* Reemer, sp. nov.**

8 Tergite 2 (except for yellow maculae) reddish at least on apical 1/2 (Fig. 30). Mesoscutum reddish with a median black vitta of ~ 1/3 the width of the scutum (Fig. 31) ....***P. brunettii* Reemer**

– Tergite 2 (except for yellow maculae) black, at most narrowly reddish along posterior margin (Figs 54, 55). Mesoscutum dark brown to blackish, at most with pale colouration along margin (Fig. 58)................................**9**

---

[*] Note: an undescribed species from Malaysia, only known from photographs, also keys out here. See Figs 1–3 for photos and a brief diagnosis.

9 Tergite 2 with posterior margin narrowly reddish. Postalar callus dark. Wing entirely clear. Male: Postpedicel 8× as long as scape....***P. yunnanensis* Cheng**

– Tergite 2 with posterior margin entirely dark brown (Fig. 55). Postalar callus yellow. Wing with infuscate apical 1/2 of cells r1 and r2+3 (Fig. 59). Male: Postpedicel 6× as long as scape .... ***P. halmaherensis* Reemer, sp. nov.**

10 Postpedicel shorter than scape (Fig. 13)...........................***P. luxor* (Curran)**

– Postpedicel longer than scape (Fig. 14) **11**

11 Transverse suture incomplete, medially interrupted. Metanepisternum bare. Tergite 2 with pair of elongate yellow maculae, which are either entirely separated or connected anteriorly (Figs 23, 24) **13**

– Transverse suture complete, medially not interrupted. Metanepisternum setulose. Tergite 2 with wide, continuous yellow fascia (Figs 17, 18).....**12**

12 Femora entirely yellow. Vein M1 recurrent at more or less right angle (Fig. 15). Tergite 2 constricted less strongly (Fig. 17). Wing cell r4+5 bare at basal 1/4 to 1/3...***P. contracta* (Brunetti)**

– Femora partly black. Vein M1 recurrent at acute angle (Fig. 16). Tergite 2 constricted more strongly (Fig. 18). Wing cell r4+5 entirely microtrichose ....***P. conveniens* (Brunetti)**

13 Tergites 3 and 4 yellow with pattern of black vittae (Fig. 95). Mesoscutum largely yellow, with two small black maculae posterior to postpronotum and two elongate narrow black maculae between transverse suture and posterior margin (Fig. 21) ....***P. sacki* Reemer & Ståhls**

– Tergites 3 and 4 black with yellow posterior margin (Fig. 74, 118, 123). Mesoscutum usually largely black, often with narrow or wide yellow margins, sometimes also with yellow median line and yellow fascia along transverse suture (Figs 22, 73)..**14**

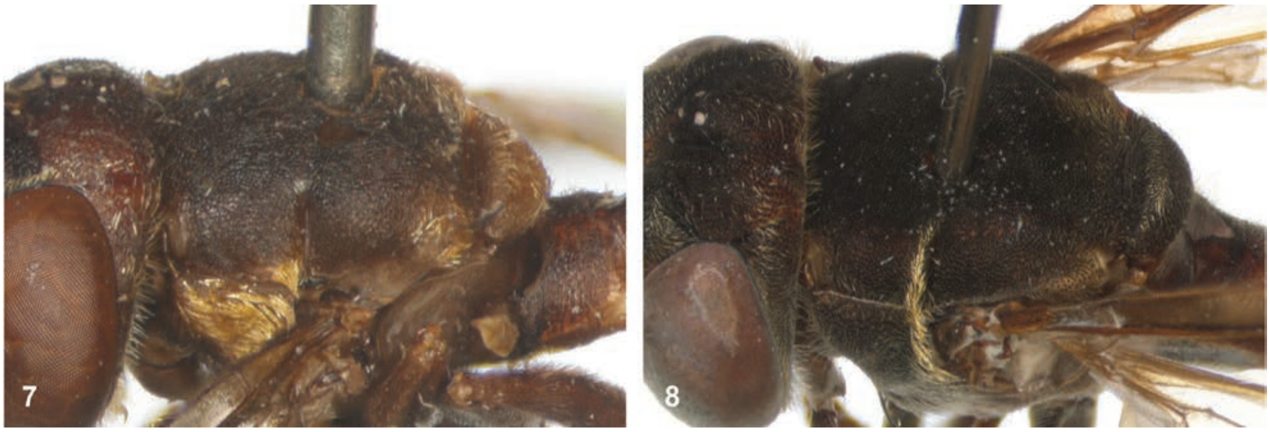
14 Tergite 2 at posterior margin narrower than median length of tergite (Fig. 23). Vertex with setulae at least twice as long as diameter of ocelli (Fig. 25). Scutellum entirely yellow (Fig. 23). Katatergite entirely dark. Male genitalia: surstylus baso-ventrally with a hook-like process (Fig. 135) ....***P. jubata* Reemer, sp. nov.**

– Tergite 2 at posterior margin wider than median length of tergite (Fig. 24). Vertex with setulae approximately as long as diameter of ocelli (Fig. 26). Scutellum with anterior margin dark (Fig. 123). Katatergite yellow with dark macula posteriorly. Male genitalia: surstylus baso-ventrally rounded (Figs 136, 137)...**15**

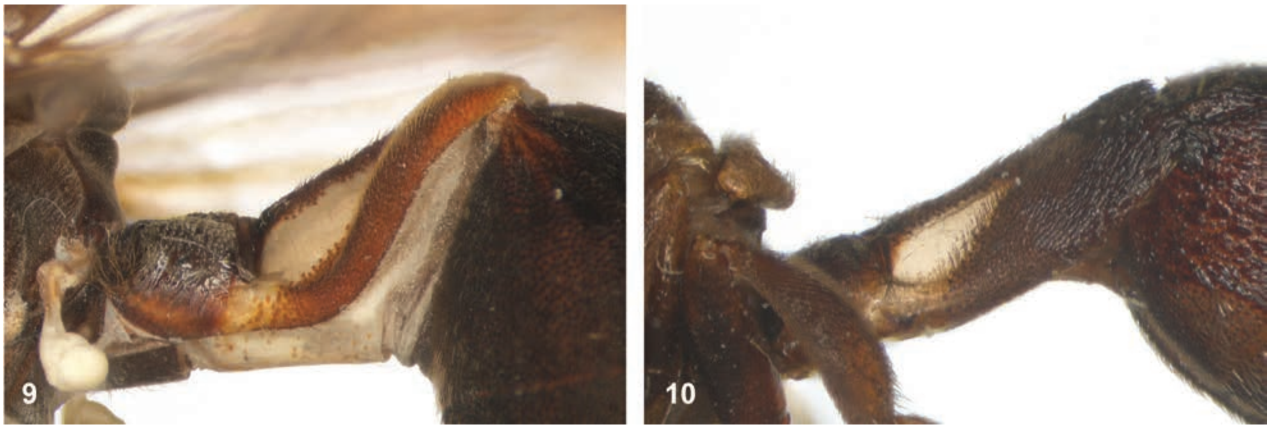
15 Mesoscutum with lateral yellow vitta continuous from postpronotum to postalar callus, although often narrower posteriad of transverse suture (Fig. 27). Male: postpedicel 4.4–5.6× as long as scape. Male genitalia as in Fig. 136 ....***P. indica* (Doleschall)**

– Mesoscutum with lateral yellow vitta interrupted posteriad of transverse suture (Fig. 28). Male: postpedicel 3.3–3.7× as long as scape. Male genitalia as in Fig. 137 ....***P. vespiformis* (de Meijere)**

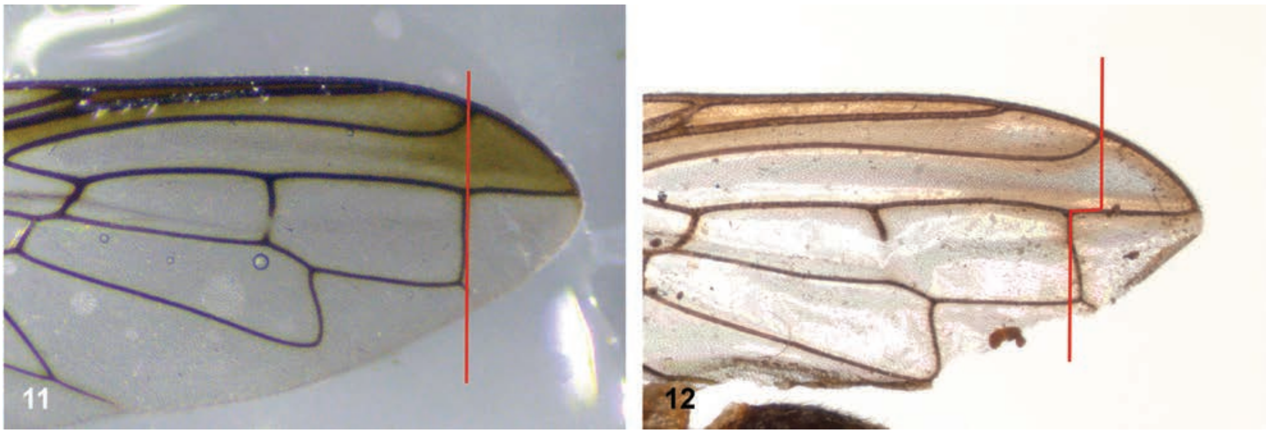
Figures 5, 6. Head, dorsolateral: **5** frons more or less even, without lateral bulges (*Paramixogaster vespiformis* female, Indonesia) **6** frons uneven, with lateral bulges (*P. icariiformis* female, neotype).



Figures 7, 8. Scutum, dorsolateral: **7** transverse suture without fascia of golden setulae (*Paramixogaster halmaherensis* Reemer, sp. nov. male, holotype) **8** transverse suture with fascia of golden setulae (*P. icariiformis* female, neotype).



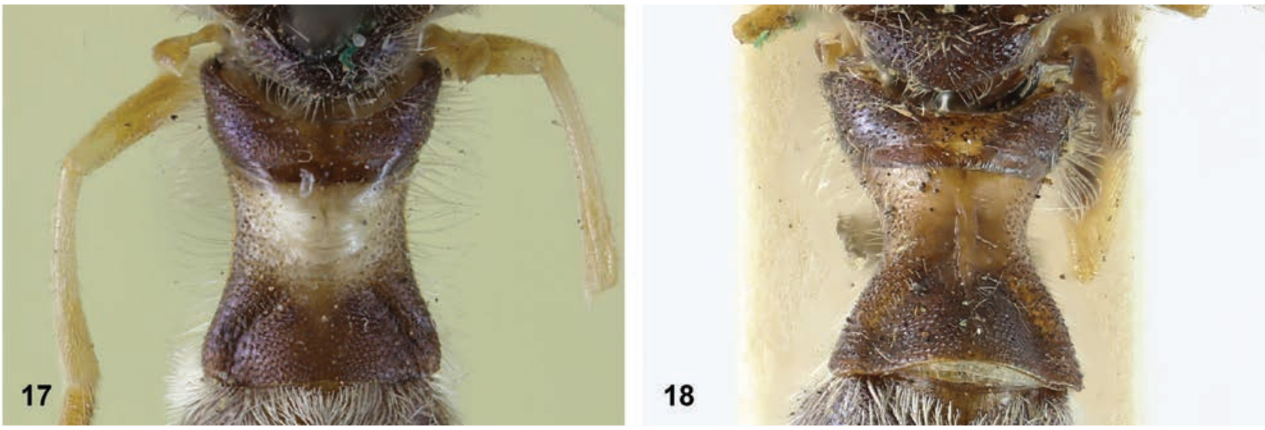
Figures 9, 10. Tergite 2, lateral: **9** *Paramixogaster icariiformis* female, neotype **10** *P. halmaherensis* Reemer, sp. nov. male, holotype.



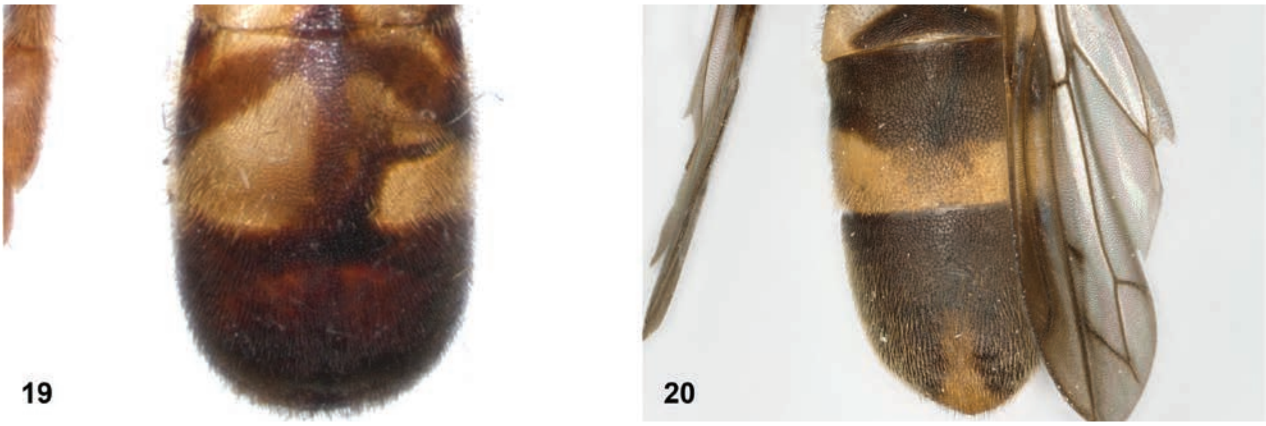
Figures 11, 12. Position of apex of vein R_{2+3}: **11** at approximately same level as joint M_1 with R_{4+5} (*Paramixogaster huoi* Reemer, nom. nov. holotype) **12** more distal than joint of M_1 with R_{4+5} (*P. sulawesiana* Reemer, sp. nov. holotype).

Figures 13, 14. Ratio of antennal segments: **13** postpedicel shorter than scape (*Paramixogaster* cf. *luxor* female, Sabah) **14** postpedicel longer than scape (*P. vespiformis* male, Sumatra).

Figures 15, 16. Apex of wing: **15** vein M_1 recurrent at more or less right angle with R_{4+5} (*Paramixogaster contracta* holotype) **16** vein M_1 recurrent at acute angle (*P. conveniens* holotype).



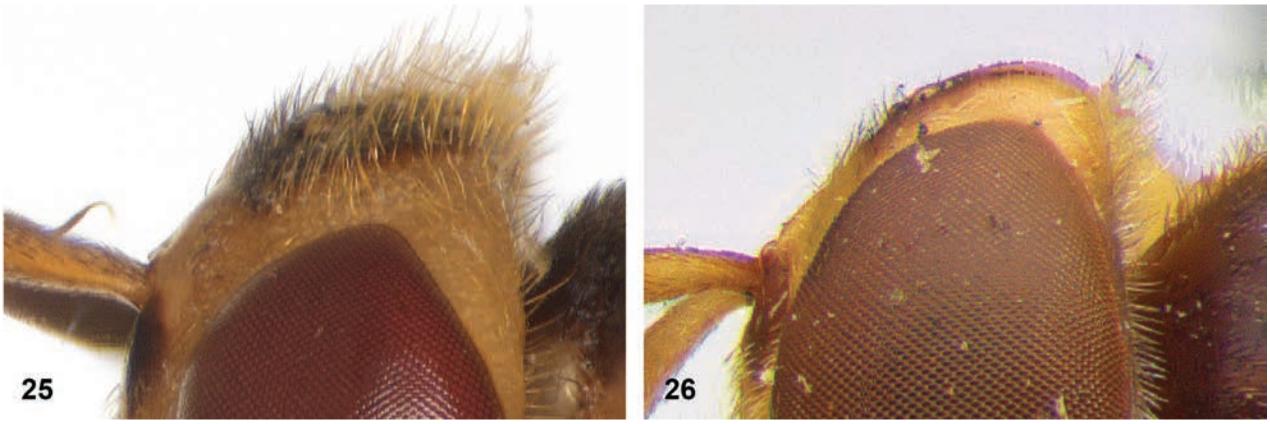
Figures 17, 18. Tergite 2 dorsal: **17** *Paramixogaster contracta* female, holotype **18** *P. conveniens* female, holotype.



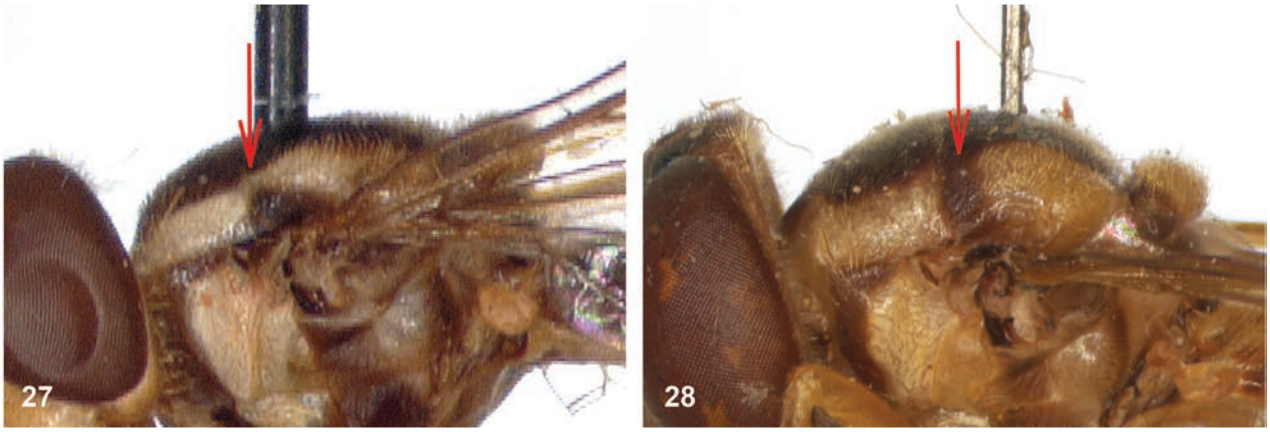
Figures 19, 20. Tergites 3 and 4 dorsal: **19** *Paramixogaster sacki* male, Taiwan **20** *P. indica* male, Ambon.

Figures 21, 22. Mesoscutum dorsal: **21** largely yellow with two four black maculae (*Paramixogaster sacki* male, Taiwan) **22** largely black with yellow margins (*P. indica* male, Ambon).

Figures 23, 24. Tergite 2 dorsal: **23** posterior margin narrower than median length of tergite (*Paramixogaster jubata* Reemer, sp. nov. male, holotype) **24** posterior margin wider than median length of tergite (*P. vespiformis* (de Meijere), lectotype).



Figures 25, 26. Vertex lateral: **25** setulae at least twice as long as diameter of ocelli (*Paramixogaster jubata* Reemer, sp. nov. male, holotype) **26** setulae approximately as long as diameter of ocelli (*P. vespiformis* female, Java).



Figures 27, 28. Mesoscutum lateral: **27** lateral yellow vitta continuous from postpronotum to postalar callus (*Paramixogaster indica*) **28** lateral yellow vitta interrupted posteriad of transverse suture (*P. vespiformis*).

Species accounts

Paramixogaster brunettii Reemer in Reemer & Ståhls, 2013

Figs 29–31

Mixogaster vespiformis Brunetti, 1913: 169. Holotype ♂: India (ZSI) [photographs studied] (secondary homonym of *Microdon vespiformis* de Meijere, 1908, see Reemer and Ståhls 2013a).

Paramixogaster vespiformis (Brunetti) – Brunetti 1923: 320; Knutson et al. 1975: 373.

Paramixogaster brunettii Reemer, 2013 in Reemer & Ståhls, 2013a: 144.

Studied type specimens. ***Holotype*** of *Mixogaster vespiformis* Brunetti, 1913. India • 1 ♂; N.E. Assam, Dibrugarh; 17–19 Nov. 1911; ZSI. Label 1: "Ind. Mus. // Dibrugarh // N.E. Assam // Abor Exped // 17–19-XI-11. // Kemp [printed vertically on left side of label]"; label 2: "Mixogaster // vespiformis // Brun. Typ. ♀"; label 3: "Paramixogas- // ter. // vespiformis // Brun Type ♀ // det. Brun. 1923"; label 4: "2177 // [illegible 2 digit code]" [digital images studied].

Diagnosis. Only male known. Body length: 8 mm. A reddish-brown species with lateral bulges on the frons. From most other species with lateral bulges on the frons, it differs by the combination of the following characters: tergite 2 less than twice as long as wide, mesoscutum without fascia of golden setulae along transverse suture. This species is most similar to *P. halmaherensis* and *P. yunnanensis*, but differs because the mesoscutum is reddish with a median black vitta of ~ 1/3 of the width of the scutum (mostly dark brown to blackish in the other two species), and tergite 2 is reddish at least on the apical 1/2 (at most narrowly reddish along posterior margin in the other two species).

Notes. *Mixogaster vespiformis* Brunetti, 1913 was included in *Paramixogaster* by Brunetti (1923). The species name became a secondary homonym when *Microdon vespiformis* de Meijere, 1908 was transferred to *Paramixogaster* by Reemer and Ståhls (2013a), who introduced the replacement name *Paramixogaster brunettii* Reemer, 2013. The type specimen itself has not been studied by the authors, but digital images were kindly provided by Jeroen van Steenis.

Distribution. Only known from Assam (India).

Paramixogaster contracta (Brunetti)

Figs 15, 17, 32–38, 119–116, 130

Microdon contractus Brunetti, 1923: 310. Holotype ♀: India (NHMUK) [examined]; Knutson et al. 1975: 370.

Paramixogaster contractus (Brunetti) – Reemer and Ståhls 2013a: 145.

Microdon subpetiolatus Thompson, 2020: 87. Syn. nov., comb. nov. Holotype ♂: Sri Lanka, Ratnapura District, Singharaja Forest (USNM) [examined].

Studied type specimens. ***Holotype*** of *Microdon contractus* Brunetti, 1923. India • 1 ♀; Deesa; 1922; C.G. Nursee leg.; NHMUK. Label 1 (round, red-bordered): "Holotype"; label 2: "Deesa // P.T.O // 3. 97."; label 3: "India: // Pres. by // Col. C.G. Nurse. // 1922 309."; label 4: "Microdon // contractus // Brun Type [female] // det. Brun. 1921".

Holotype of *Microdon subpetiolatus* Thompson, 2020. Sri Lanka • 1 ♂; coll. USNM. Label 1: "SRI LANKA: Rat. Dist. // Singharaja forest // 5 VIII 1973 600 ft. // Ginter Ekis"; label 2: "collected // in Malaise // trap"; label 3 (large, orange): "Holotype // Microdon // subpetiolatus // Thompson '19"; label 4 (with QR-code): "USNMENT // 01541885".

Paratype of *Microdon subpetiolatus* Thompson, 2020. Sri Lanka • 1 ♂; coll. USNM. Label 1: "SRI LANKA: Tri. Dist. // Trincomalee, China // Bay Ridge Bungalow // 0–100', 13–17-V-1976"; label 2: "Collected by // K.V. Krombein // P.B. Karunaratne // S. Karunaratne // D.W. Balasooriya"; label 3: "Microdon // 08-03 // det. // FC Thompson 19"; label 4 (yellow): "Paratype // Microdon // subpetiolatus // FCT-2010"; label 5 (with QR-code): "USNMENT // 01541884".

Diagnosis. Body length: male 7.5 mm, female 9 mm. This species and *P. conveniens* share a unique character among Microdontinae: a setulose metanepisternum. Within *Paramixogaster*, both species also stand out because of the complete transverse suture on the mesoscutum. *Paramixogaster contracta* differs from *P. conveniens* in the following characters: legs entirely yellow (femora partly black in *P. conveniens*) and vein M_1 recurrent at more or less right angle (acute angle in *P. conveniens*). Male genitalia as in Fig. 130.

Redescription (based on holotype of *M. contractus* Brunetti). Adult female. Body length: 9 mm.

***Head*.** Face occupies 45% of head width in frontal view, with sides below antennae parallel; black; entirely white setulose. Gena widely developed; black; white setulose. Oral margin not notched anteriorly, laterally not produced. Frons and vertex blackish brown; white setulose. Ocellar triangle not elevated. Occiput black; white setulose. Eye very sparse and short setulose, almost bare. Antennal fossa approximately as high as wide. Antenna dark brown, scape paler; postpedicel ~ 1.25× as long as scape. Postpedicel parallel-sided with rounded apex; with small sensory pit at apical 1/3. Arista slender, ~ 1/2 as long as postpedicel.

***Thorax*.** Mesoscutum shining blackish brown; entirely white setulose. Postpronotum pale brown; bare. Postalar callus pale brown; white setulose. Scutellum shining blackish brown; white setulose. Anepisternum with shallow sulcus separating posterior from anterior part; blackish; white setulose, with small bare part ventro-medially. Anepimeron blackish; entirely white setulose. Katepisternum blackish brown; white setulose dorsally; bare ventrally. Katatergite pale brown; long microtrichose. Anatergite pale brown; short microtrichose. Calypter and halter yellow.

Wing: hyaline; microtrichose, except bare on cells bc and c, basal 3/5 of cell r_1, basal 1/4 of cell r_{2+3}, basal 1/3 of cell r_{4+5}, antero-basal 1/6 of cell dm, entirely on cells br and bm, basal 2/3 of cell cup, and medially on alula.

Legs: Pale yellow; yellow to white setulose.

***Abdomen*.** Tergite 2 constricted and tergites 3 and 4 widened; narrowest point at anterior 1/4 of tergite 2, widest at posterior margin of tergite 3. Tergites blackish brown, except anterior 1/2 of tergite 2 pale yellow; white setulose, except with short brown setulae on posterior 1/2 of tergite 2 and posterior 2/3 of tergite 3, with white setulae long and conspicuous on anterior 1/3 of tergite 3 and anterior 1/2 of tergites 4 and 5. Tergite 2 with median tubercle on anterior 1/3. Sternites pale brown; yellow setulose.

Male (based on holotype and paratype of *M. subpetiolatus* Thompson).

As female, except for following differences. Body length: 7.5 mm. Face occupies 42–46% (*n* = 2) of head width in frontal view. Postpedicel 1.2–1.4× as long as scape (*n* = 2).

Notes. The type specimen of *Microdon contractus* Brunetti (a female) (Figs 32–38) was compared to those of *M. subpetiolatus* Thompson (male holotype and male paratype: Figs 109–116). They were found to be very similar, except for some differences usually associated with sexual dimorphism, such as a slightly wider abdomen in the female. No differences were found that could support specific taxonomic status for both taxa, so they are here considered as synonyms, with *M. subpetiolatus* Thompson syn. nov. as the junior synonym.

Distribution. Known from India (Gujarat: Deesa) and Sri Lanka.

***Paramixogaster conveniens* (Brunetti, 1923)**

Figs 39–45

Microdon conveniens Brunetti, 1923: 311. Holotype ♀: India (NHMUK) [examined]; Knutson et al. 1975: 370.

Paramixogaster conveniens (Brunetti) – Reemer and Ståhls 2013a: 145.

Studied type specimens. ***Holotype*** of *Microdon conveniens* Brunetti. India • 1 ♀; Assam; Cameron leg.; NHMUK. Label 1 (round, red-bordered): “Holotype”; label 2: “Assam.”; label 3: “Cameron Coll. // 1902-105”; label 4: “M. conveniens // Brun. Type. [female] // det. Brun. 1923”.

Diagnosis. Only female known. Body length: 9.5 mm. This species and *P. contracta* share a unique character among Microdontinae: a setulose metanepisternum. Within *Paramixogaster*, both species also stand out because of the complete transverse suture on the mesoscutum. *Paramixogaster conveniens* differs from *P. contracta* in the following characters: legs with femora partly black (entirely yellow in *P. contracta*) and vein M1 recurrent at acute angle (more or less right angle in *P. contracta*).

Redescription (based on holotype). Adult female Body length: 9.5 mm.

***Head*.** Face occupying ~ 1/3 of head width in frontal view, with sides more or less parallel below antennae; black; entirely white setulose. Gena widely developed; black; white setulose. Oral margin not notched anteriorly, laterally not produced. Frons and vertex black; yellowish white setulose. Ocellar triangle not elevated. Occiput black; white setulose. Eye bare. Antennal fossa approximately as high as wide. Antenna: scape brown [other segments are missing in type specimen].

***Thorax*.** Mesoscutum shining black, brownish along margins; entirely white setulose. Postpronotum pale brown; bare. Postalar callus pale brown; white setulose. Scutellum shining blackish brown; white setulose. Anepisternum with shallow sulcus separating posterior from anterior part; blackish brown; white setulose, except bare on narrow strip along anterior margin. Anepimeron blackish brown; entirely white setulose. Katepisternum blackish brown; white setulose dorsally; bare ventrally. Katatergite brown; long microtrichose. Anatergite brown; short microtrichose. Calypter and halter brownish yellow.

Wing: hyaline; microtrichose, except bare on cell bc and basal 1/3 of cell c, basal 1/4 of cell r_1, basal 2/3 of cell br, basal 1/2 of cell bm, basal 1/2 of cell cup, and baso-median 1/2 of alula.

Legs: Pale yellow, except hind femur dark brown on basal 3/4 and hind tibia with brown ring on apical 1/3; yellow to white setulose.

***Abdomen*.** With tergite 2 constricted and tergites 3 and 4 widened; narrowest point at anterior 1/4 of tergite 2, widest at posterior margin of tergite 3. Tergites blackish brown, except anterior 1/2 of tergite 2 yellow; entirely white setulose, with setulae long and conspicuous on anterior 1/4 of tergite 3, anterior 1/3 of tergite 4 and on most of tergite 5. Sternites brown, white setulose.

Distribution. Only known from Assam (India).

Paramixogaster fujianensis Cheng in Huang & Cheng, 2012

Paramixogaster fujianensis Cheng in Huang & Cheng, 2012: 695. Holotype ♂: China, Yunnan (CASB, but see notes) [not examined]; Reemer and Ståhls 2013a: 145.

Diagnosis. Only male known. Body length: male 12 mm. Among the species with lateral bulges on the frons (which may not be as clear in this species as in other ones), *P. fujianensis* is the only one in which tergite 2 is more than twice as long as wide (Huang and Cheng 2012: fig. 415). The mesonotal transverse suture is incomplete. According to the English translation of the description, the postpedicel is 3× as long as the scape (Huang and Cheng 2012). Figures of habitus and head are provided by Huang and Cheng (2012). Note that these characters are based on the description only and could not be verified against any specimens.

Notes. Unsuccessful attempts were made to locate the type specimen of *Paramixogaster fujianensis* by trying to contact the author and by enquiring at the CASB collection (Ke-Ke Huo pers. comm. 2023). The original description by Huang and Cheng (2012) is in Chinese, but the same work also provides an English translation, as well as figures of the head in frontal view and of the thorax and abdomen in dorsal view. This information makes clear that this species is distinct from all other known Oriental species of *Paramixogaster*, especially in the very elongate tergite 2.

Paramixogaster halmaherensis Reemer, sp. nov.

https://zoobank.org/00A93B1B-3A27-4B8B-A79F-B87A1E70B955
Figs 54–59, 131

Type material. *Holotype*. INDONESIA • 1 ♂; Halmahera, Dodinga (sealevel); 2–4 Nov. 1951; coll. RMNH. Label 1: “Isl. halmaheira // Dodinga (sealevel) // 2,4-XI-1951 // Native Collector”; label 2: “Mus. Zool. Bogor // Microdon ves- // piformis de Meijere // Det. Adisoemarto”; label 3 (red): “HOLOTYPE // Paramixogaster // halmaherensis // Reemer 2024”.

Diagnosis. Only male known. Body length: 8 mm. This is one of the three species with a swollen frons with lateral bulges (Figs 56, 57) and without golden setulae along the transverse suture on the scutum (Fig. 58) (the other two are *P. brunettii* and *P. yunnanensis*). From *P. brunettii* it differs because tergite 2 is black (reddish in *P. brunettii*) with a pair of yellow maculae. From *P. yunnanensis* it differs by the yellow postalar calli (dark in *P. yunnanensis*), postpedicel 6× as long as scape (8× as long as scape in *P. yunnanensis*), and the infuscate apical 1/2 of wing cells r_1 and r_{2+3} (wing entirely clear in *P. yunnanensis*). Male genitalia as in Fig. 131.

Description (based on holotype). Adult male. Body length: 8 mm.

***Head*.** Face occupying ~ 1/2 of head width in frontal view, with sides somewhat converging ventrad; brown with widely yellow lateral and ventral margins; golden yellow setulose except for narrow median bare line. Gena yellow; yellow setulose. Oral margin not notched anteriorly, laterally weakly produced. Frons posteriorly with blackish pair of lateral bulges which are short black setulose, separated by narrow pale brown crease; anteriorly with pair of slightly concave areas which are yellow setulose, separated from face by pair of shiny black bare maculae. Vertex swollen; brown; short black setulose. Occiput yellow, somewhat darker dorsally and ventrally; white setulose. Eye bare. Antennal fossa approximately as high as wide. Antenna orange-brown; postpedicel ~ 6× as long as scape. Arista slender, yellow, a little longer than the scape.

***Thorax*.** Mesoscutum blackish brown with lateral and posterior margins somewhat paler; short black setulose, except for small patch of golden yellow setulae anterior to notopleuron and large patch of pale yellowish setulae anterior to scutellum. Postpronotum pale brown, bare. Postalar callus yellow, yellow setulose. Scutellum without calcars; yellow; yellow setulose. Pleura yellowish brown. Anepisternum entirely covered with thick golden yellow setulae, appressed and directed hindward. Katepisternum long golden yellow setulose dorsally; bare ventrally. Katepimeron with a few long yellow setulae. Katatergite and anatergite short microtrichose. Metanotum shining brown. Calypter greyish yellow. Halter yellow.

Wing: hyaline; microtrichose, except bare in cell r_1 narrowly along Rs, basal 1/3 of r_{4+5}, entirely on br (except for microtrichia along vena spuria), antero-basal 1/4 of dm, entirely on bm, basal 2/3 of cup.

Legs: yellowish brown, except mid-femora and hind-legs darker brown; yellow setulose.

***Abdomen*.** Constricted basally, narrowest at transition between tergites 1 and 2, widest at transition between tergites 3 and 4. Tergite 1 dark brown; short white setulose, except long black setulose at antero-lateral callus. Tergite 2 dark brown with two large, elongate, pale yellow maculae from anterior margin to ~ 1/2 of tergite; short black setulose, except bare on yellow maculae and narrowly yellow setulose along lateral margin. Tergite 3 dark brown; black setulose except for triangular patch of white setulae at postero-lateral corners. Tergite 4 dark brown; short black setulose with sparse longer golden yellow setulae intermixed and with patch of white setulae at antero-lateral corners. Sternite 1 brown; short black setulose. Sternite 2 yellow; bare. Sternites 3 and 4 brown; short black setulose. Genitalia as in Fig. 131.

Distribution. Only known from Halmahera (Indonesia).

Etymology. The specific epithet is to be treated as a noun and refers to the type locality.

Paramixogaster huoi **Reemer, nom. nov.**

Figs 11, 60–66

Paramixogaster trifasciatus Huo & Zhao in Zhao & Huo, 2022: 4; primary homonym of *Paramixogaster trifasciatus* Ssymank & Reemer, 2016: 404.

Studied type specimens. ***Holotype*** of *Paramixogaster trifasciatus* Huo & Zhao. CHINA • 1 ♂, Guangdong, Shenzhen City, Wutong Mountains; 114°21'E, 22°57'N; 927 m above sea level; 25 April 2020; Zuqi Mai leg.; coll. SUHC [only photos studied].

Diagnosis. Only male known. Body length: 7 mm. It belongs to the group of species with lateral bulges on the frons (Figs 63, 64). From *P. fujianensis* it differs by tergite 2 being < 2× as long as wide (> 2× as long as wide in *P. fujianensis*). From *P. icariiformis* it differs by the presence of fasciae of golden setulae along the posterior margins of tergites 3 and 4 (absent in *P. icariiformis*). There is a continuous fascia of golden setulae along the mesoscutal transverse suture, and also along the posterior margin of the scutum, and there are fasciae of golden setulae along the posterior margins of tergites 3 and 4 (Figs 60–62). These fasciae are not as dense and sharply demarcated as in *P. kodaiana* Sankararaman & Reemer, sp. nov., but more similar to those in *P. sulawesiana* Reemer, sp. nov. From the latter species, *P. huoi* Reemer, nom. nov. differs by the colouration of the face, which is yellow with a vaguely darker median vitta (mostly dark with lateral margins yellow in *P. sulawesiana* Reemer, sp. nov.), and the wing venation: the apex of R_{2+3} is situated at approximately the same level as the joint of M_1 with R_{4+5}. (more distal than joint of M_1 with R_{4+5} in *P. sulawesiana* Reemer, sp. nov.).

Notes. The name *Paramixogaster trifasciatus* was already used by Ssymank and Reemer (2016) for an African species. When Huo and Zhao (in Zhao and Huo 2022) described a new species from China under the same name, a primary homonym was created. As a replacement name, *Paramixogaster huoi* Reemer, nom. nov. is proposed here, in honour of Ke-Ke Huo, one of the original authors, who was kind enough to provide photographs of the holotype.

Paramixogaster icariiformis **Pendlebury, 1927**

Figs 6, 8, 9, 67–72

Paramixogaster icariiformis Pendlebury, 1927: 38. Holotype ♀: Malaysia, Selangor, Bukit Kuta (lost); Knutson et al. 1975: 373; Reemer and Ståhls 2013a: 145.

Studied type specimens. ***Neotype*** of *Paramixogaster icariiformis* Pendlebury (new neotype designation, see notes). Thailand • 1 ♀; Loei, Phu Ruea NP Sa Sawan, 17°30.735'N, 101°20.601'E, alt. 1352 m asl., 12–10 March 2007; leg. Patikhom Tumtpip; coll. QSBG. Label 1: "THAILAND Loei, Phu Ruea NP Sa Sawan, // 17°30.735'N, 101°20.601'E, 1352 m, // Malaise trap, 12–19.iii.2007, Patikhom // Turntip leg. T2309"; label 2: "MR315 // DNA-voucher // Y1076"; label 3 (red): "NEOTYPE // *Paramixogaster* // *icariiformis* Pendlebury, 1927 // Designated by Reemer & // Sankararaman 2024.

Diagnosis. Only female known. Body length: 11 mm. This is the only known Oriental species of *Paramixogaster* that is entirely black except for tergite 2 red (Figs 67, 68). Another unique character of this species is the 'saddle-like' shape of tergite 2, due to its lateral margins being strongly curved upward posteriorly (Figs 9, 72).

Redescription (based on neotype). Adult female. Body size: 11 mm.

Head. Face at level of antennae occupying ~ 0.6 of head width in frontal view, with sides quite strongly converging ventrad; brown, more blackish in dorsolateral depressed areas, narrowly pale yellow ventrally close to oral gena; white setulose medially, golden yellow setulose laterally. Gena black; white setulose. Frons with blackish pair of lateral bulges which are short golden yellow setulose, separated by narrow pale brown triangular depression. Vertex swollen; black; short black setulose medially, short yellow setulose laterally and posteriorly. Occiput black; yellow setulose dorsally, white setulose ventrally. Eye bare. Antennal fossa slightly wider than high. Antenna brown; postpedicel ~ 4× as long as scape. Arista slender, yellow, ~ 2× as long as scape.

Thorax. Mesoscutum black; short black setulose, except for narrow fascia of golden yellow setulae along transverse suture of 1/5 of width of mesoscutum, and patch of yellowish setulae of approximately the size of the scutellum anterior to scutellum. Postpronotum brown, bare. Postalar callus yellow, yellow setulose. Scutellum without calcars; black; yellow setulose. Pleura dark brown. Anepisternum and anepimeron white setulose, except for narrow fascia of golden yellow setulae along postero-dorsal margin, which is connected to the fascia of golden yellow setulae along the transverse suture of the mesoscutum. Katepisternum long white setulose dorsally; bare ventrally. Katepimeron with a few long white setulae. Katatergite and anatergite short microtrichose. Metanotum brown. Calypter pale grey. Halter white.

Wing: infuscate anteriorly from costal vein to vena spuria and anterior 1/3 of cell r_{4+5}; microtrichose, except bare in cell br posteriad of vena spuria, all of bm, postero-basal 1/4 of cell r_{4+5}, antero-basal 1/4 of dm, most of cup except microtrichose in distal corner, most of alula except microtrichose along margins.

Legs: pale brown, except hind femur and hind tibia dark brown; white setulose.

Abdomen. Constricted basally, narrowest at basal 1/4 of tergite 2, widest at around 1/2 of tergite 3. Tergite 1 dark brown; white setulose. Tergite 2 with lateral margins strongly curved upward posteriorly; orange-brown with two large, elongate, pale yellow maculae from anterior margin to just more than half of tergite; short golden yellow setulose, more densely so along posterior margin, with black setulae between yellow maculae and bare on these maculae. Tergite 3 black; very short black setulose except for longer whitish setulae sparsely intermixed laterally. Tergite 4 as tergite 3, except narrowly yellow laterally along posterior margin. Tergite 5 black with yellow lateral and posterior margins; black setulose on black parts, yellow setulose on yellow parts. Sternite 1 brown; sparsely yellow and black setulose. Sternite 2 whitish yellow; sparsely yellow and black setulose. Sternites 3–5 blackish; white setulose.

Notes. The original type of this species is registered to be in the collection of the NHMUK (Evenhuis and Pape 2022), but it is not there (N. Wyatt pers. comm. 2022). Probably this type is lost. However, the description by Pendlebury (1927) agrees very well with the female specimen from Thailand here designated as neotype. According to Pendlebury (1927), this is an entirely black species except for the reddish tergite 2. There are not fasciae of yellow or golden setulae on the thorax or abdomen. No other known species of *Paramixogaster* have the same colouration (entirely black with red tergite 2).

Distribution. Malaysia and Thailand.

Paramixogaster indica **(Doleschall, 1857)**

Figs 20, 22, 123–129, 136

Ceratophya indica Doleschall, 1857: 404. Holotype: Indonesia, Ambon (HNHM, lost) [not examined].

Microdon indicus (Doleschall, 1857) – Thompson and Vockeroth 1989: 438.

Paramixogaster indicus (Doleschall, 1857) – Reemer and Ståhls 2013a: 145.

Paramixogaster wegneri Keiser, 1964: 84. Syn. nov. Holotype ♂: Indonesia, Maluku, Ambon (NMB) [examined]; Knutson et al. 1975: 374; Thompson and Vockeroth 1989: 439; Reemer and Ståhls 2013a: 145.

Studied type specimens. ***Holotype*** of *Paramixogaster wegneri* Keiser. INDONESIA • 1 ♂; label 1 (red): “TYPUS”; label 2 (pale green): “INDONESIA // AMBON // 6.I.61 // A.M.R. WEGNER”; NMB.

Paratype of of *Paramixogaster wegneri* Keiser. INDONESIA • 1 ♀; Ambon; 1 Jan. 1961; A.M.R. Wegner leg.; NMB.

Paratypes of of *Paramixogaster wegneri* Keiser. INDONESIA • 5 ♂; Ambon; 5 different collection dates: 29 Oct. 1960, 23 Nov. 1960, 8 Dec. 1960, 12 Dec. 1960, 11 Jan. 1961; A.M.R. Wegner leg.; NMB.

Additional specimens. INDONESIA • 2 ♂ 2 ♀; Buru; 7 Dec. 1921; L.J. Toxopeus leg.; RMNH; 1 ♀; Buru; 8 Dec. 1921; L.J. Toxopeus leg.; RMNH • 1 ♀; Ambon [no further data]; NHMUK • 1 ♀; West Papua, Fak-Fak; A.E. Pratt leg.; NHMUK [013933418].

Diagnosis. Body length: males 7.5–9.5 mm (*n* = 8), females 9–11 mm (*n* = 6). This belongs to the group of species without lateral bulges on the frons. From *P. luxor* it differs by the postpedicel being longer than the scape (shorter in *P. luxor*). From *P. contracta* and *P. conveniens* it differs by the incomplete transverse suture (complete in *P. contracta* and *P. conveniens*). From *P. sacki* it differs by tergites 3 and 4 being black with yellow posterior margin (yellow with pattern of black vittae in *P. sacki*). It differs from *P. jubata* Reemer, sp. nov. by the shorter tergite 2, of which the posterior margin is wider than the median length (longer in *P. jubata* Reemer, sp. nov.), the dark anterior margin of the scutellum (entirely yellow in *P. jubata* Reemer, sp. nov.) and the shorter setulae on the vertex.

Paramixogaster indica is most similar to *P. vespiformis*, from which it differs by the continuous yellow vitta between postpronotum and posterior callus (interrupted in *P. vespiformis*), and the longer postpedicel in the male, which is 4.4–5.6× as long as the scape (3.3–3.7× as long in *P. vespiformis*). Male: postpedicel 4.4–5.6× as long as scape (*n* = 6). Female: postpedicel 2.4–2.9× as long as scape (*n* = 5). The degree of infuscation of wing apex is very variable. Male genitalia as in Fig. 136.

Notes. No type specimen of *Ceratophya indica* Doleschall is known. However, the description and illustration of this species from Ambon by Doleschall (1857) correspond well to the studied type specimens of *Paramixogaster wegneri* by Keiser (1964), which was also described from Ambon. Keiser (1964) does not mention *P. indica*, so probably he was unaware of it. Based on the descriptions and illustrations, these taxa share the following characters: postpedicel 4–6× longer than scape, face, and vertex partly yellow, mesoscutum black, wing with infuscate apex, tergite 2 narrowest at base and with two apically diverging yellow vittae, tergites 3 and 4 black with yellow hind margins. Based on these similarities and the shared type locality (Ambon), *P. wegneri* Keiser syn. nov. is here considered to be a junior synonym of *Ceratophya indica* Doleschall.

This species is very closely related to *P. vespiformis* (de Meijere). The differences between these taxa are small but consistent.

Distribution. Known from eastern parts of Indonesia, east of the Wallace Line: the Maluku islands of Ambon and Buru, and West Papua. Specimens were collected between October and January.

Paramixogaster jubata Reemer, sp. nov.

https://zoobank.org/DDEE3975-7CDC-4B9D-A6AB-59ED50BAB188
Figs 23, 25, 73–80, 135

Type material. *Holotype*. Vietnam • 1 ♂, holotype of *Paramixogaster jubata* sp. nov. Reemer; S. Vietnam, Dông Nai, Cat Tien National Park; alt. 100 m.; 13–20 May 2007; C. van Achterberg & R. de Vries leg.; RMNH. Label 1: "S. Vietnam: Dông Nai // Cat Tien N.P., ca. 100 m // 13–20.v.2007. Mal. traps // 25–29, eco-trail; C. v. Achter- // berg & R. de Vries, RMNH'07"; label 2 (red): "HOLOTYPE // Paramixogaster // jubata // Reemer 2024".

***Paratypes*.** Vietnam • 1 ♂; Cat Tien National Park; 13–20 May 2021; Malaise trap; C. van Achterberg & R. de Vries leg.; RMNH; MZH DNA voucher Y0721. [abdomen missing].

Thailand • 1 ♂; Phitsanulok T567, Thung Salaeng Luang National Park; 580 m.; 16°50.217'N, 101°52.541'E; 11–18 Aug. 2006; Malaise trap; Pongpilak Pranee leg.; QSBG.

Diagnosis. Only male known. Body length: 6–7 mm. A small species without lateral bulges on the frons and postpedicel 3.3–3.7× as long as scape (*n* = 3). In colouration it looks much like *P. indica* and *P. vespiformis*, from which it differs by the longer than wide tergite 2 (wider than long in *P. indica* and *P. vespiformis*) and the long setulae on the vertex, which are at least twice as long as the diameter of the ocelli (approximately as long as diameter of ocelli in *P. indica* and *P. vespiformis*) (Figs 25, 76). Male genitalia as in Fig. 135.

Description (based on holotype). Adult male Body size: 7 mm.

***Head*.** Face occupying ~ 2/5 of head width in frontal view, with sides slightly converging ventrad; yellow, except for brown macula laterad of antennal fossa and median brown macula of almost 1/3 of width of face; yellow setulose, except black setulose on median brown macula. Gena yellow, yellow setulose. Oral margin laterally hardly produced. Frons yellow; yellow setulose. Vertex with large median dark brown macula, yellow laterally; black setulose on brown part, yellow setulose on yellow parts. Occiput yellow, yellow setulose. Eye bare. Antennal fossa approximately as high as wide. Antenna with scape and pedicel yellow, postpedicel brown; postpedicel ~ 3.7× as long as scape. Arista slender, yellow, slightly longer than scape.

***Thorax*.** Mesoscutum black with yellow fascia along transverse suture and yellow median vitta from anterior margin to ~ 3/4 of length; mostly black setulose on black parts and yellow setulose on yellow parts, except for large median patch of longer yellow setulae on posterior 1/3. Postpronotum yellow, bare. Postalar callus yellow, yellow setulose. Scutellum without calcars; yellow; yellow setulose. Pleurae yellow, except anterior anepisternum, ventral part of posterior anepisternum, ventral katepisternum and katepimeron brown. Anepisternum with shallow sulcus separating posterior from anterior part; yellow setulose anteriorly and posteriorly, with wide bare part in between. Anepimeron entirely long yellow setulose. Katepisternum long yellow setulose dorsally; bare ventrally. Katatergite long microtrichose, anatergite short microtrichose. Metanotum shining brown. Calypter grey. Halter yellow.

Wing: hyaline; microtrichose, except bare on cell br (only with microtrichia along vena spuria), on basal 1/2 of cell bm, and basal 1/3 of cell cup.

Legs: yellow, except hind tibia and basal 2/3 of hind tibia brown; yellow setulose, except mid tibia, hind tibia, and hind femur black setulose. Coxae and trochanters dark brown.

Abdomen. Constricted basally, narrowest at tergite 1, widest halfway tergite 4. Tergite 1 blackish brown; black and yellow setulose. Tergite 2 with two long, oblique, pale-yellow maculae from anterior to posterior margin, which leave blackish brown antero-lateral corners and a blackish brown posterior triangle; mostly yellow setulose, but with some yellow setulae anteriorly and yellow setulose along lateral margin. Tergite 3 blackish brown on slightly less than anterior half, yellow posteriorly; black setulose on dark parts, yellow setulose on yellow parts. Tergite 4 blackish brown on anterior 3/5, except for median yellow triangle, which is an extension of the yellow fascia on the posterior 2/5 of the tergite; black setulose on anterior 3/5, yellow setulose on posterior 2/5. Sternite 1 yellow; bare. Sternites 2 and 3 yellow; yellow setulose. Sternite 4 yellowish with vague dark brown markings; black setulose. Genitalia as in Fig. 135.

Distribution. Thailand and Vietnam.

Etymology. The specific epithet *jubata* (Latin, adjective) means ‘with manes’. This refers to the setulae on the vertex, which are longer than in the resembling species *P. indica*.

Paramixogaster kodaiana **Sankararaman & Reemer, sp. nov.**

https://zoobank.org/D7109D90-0F62-49EF-9877-DA7014DFF8D5
Figs 81–87

Type material. *Holotype.* India • 1 ♀; Vattakanal, Kodaikanal; 2070 m a.s.l.; 10°12'54.03"N, 77°29'07.15"E; 4 January 2022; H. Sankararaman leg.; NBAIR.

Label 1: “India: Vattakanal, Kodaikanal, 10°12'54.03"N, 77°29'07.15"E // Sankararaman. H leg. 04.i.2022"; label 2 (red): “*Paramixogaster kodaiana* sp. nov. // det. Sankararaman & Reemer”.

Paratype. India • 1 ♀; Kodaikanal, Pulney Hills, S. India; 1980 m asl [6500 ft.]; April–May 1953; P.S. Nathan leg.; USNM [unique specimen identifier USNMENT01541882].

Diagnosis. Only female known. Body length: 11 mm. *Paramixogaster kodaiana* Sankararaman & Reemer, sp. nov. belongs to the group of species with lateral bulges on the frons. From *P. fujianensis* it differs by terigte 2 being less than twice as long as wide (more than twice as long as wide in *P. fujianensis*). From *P. icariiformis* it differs by the presence of fasciae of golden setulae along the posterior margins of tergites 3 and 4 (absent in *P. icariiformis*). From *P. huoi* Reemer, nom. nov. and *P. sulawesiana* Reemer, sp. nov. it differs by the medially interrupted fascia of golden setulae along the transverse suture of the scutum (continuous in *P. huoi* Reemer, nom. nov. and *P. sulawesiana* Reemer, sp. nov.).

Description (based on holotype). Adult female. Body length: 11 mm.

***Head*.** Face occupying less than 1/3 of head width in frontal view, with sides slightly converging ventrally; dark brown; golden setulose. Gena brown; golden setulose. Oral margin slightly produced laterally. Frons brown; golden setulose. Vertex brown; golden setulose. Ocellar triangle slightly elevated. Occiput wide dorso-laterally, narrowing down ventrally; brown; golden yellow setulose dorsally adjacent to vertical triangle, long silvery white setulose ventrally. Eye bare. Antennal fossa approximately as high as wide. Antenna mostly brown, scape and pedicel orange-brown, postpedicel black; ratio of lengths of scape, pedicel and postpedicel approximately as 1:0.4:4.4. Scape ~ 2.4× the length of pedicel, postpedicel 4.4× the length of scape. Arista orange-brown, slender, arising close to base of postpedicel and ~ 0.4× (2/5) of length of postpedicel.

***Thorax*.** Mesoscutum dark brown to black, golden setulose. Postpronotum black, bare, but with sparsely scattered long golden setulae, posteriorly. Mesonotum black with fine punctures; with fascia of dense golden setulae along the transverse suture (medially interrupted) and along posterior margin, including postalar calli. Scutellum without calcars; black; dense golden setulose. Pleura brown to black, with short white microtrichia. Anepisternum and katepisternum with golden setulae along posterior margin as extension of golden fascia along mesonotal transverse suture. Anepimeron short white setulose, other pleurites short brown to black microtrichia. Katepisternum blackish brown; long golden yellow setulose dorsally; bare ventrally. Katatergite brown to black; white microtrichose. Metanotum dark brown. Calypter yellow. Halter yellow.

Wing: microtrichose, except for bare regions in basal 1/5 of cells c, bc, br, almost entire bm, basal 2/3 of cup and medially on alula. Blackish antero-apically with distinct dark cloud (apical part of r_1, entire r_{2+3}, anterior part of r_{4+5}) and brownish on basal 1/2, otherwise subhyaline. Stigmal crossvein present. Alula ~ 2× as long as wide.

Legs: brown to reddish brown, with silvery white setulae. Coxae and trochanters dark brown to black with pale setulae, hind coxa with golden setulae. Hind femur dark brown to black basally. Tibiae and tarsi reddish brown.

***Abdomen*.** Segment 2 constricted and segments 3 and 4 widened; narrowest point at posterior tergite 1, widest at posterior margin of tergite 3. Tergites dark brown to black with fine punctures as in mesonotum. Tergite 1 dark brown, with long, scattered, silvery white setulae. Tergite 2 black, constricted and dorsoventrally flattened, with widely separated yellow vittae, anteriorly wide and oblique, posteriorly narrowed down and parallel not reaching the golden setulae along the posterior margin of tergite 2. Dense golden setulae on tergite 2, 3, and 4 posteriorly, scattered golden microtrichia on tergites 3, 4 and 5 dorso-laterally. Sternite 2 pale brown, short yellow setulose. Other sternites brown.

Male. Unknown.

Notes. This species is likely to mimic wasps belonging to the genus *Ropalidia* Guérin-Méneville, 1831 (Hymenoptera: Vespidae: Polistinae) by having similar colouration on wing and abdomen. The resting behavior was also very similar: the fly was perching on the underside of a leaf holding its abdomen upright with wings kept flat, as various species *Ropalidia* also do.

Habitat. The holotype was collected in montane evergreen shola forests, in proximity to human settlement. The dense vegetation included several perennial trees, ferns, and grass. The fly was found perching on the leaves of guava (*Psidium* L.).

Distribution. Only known from the type locality in Tamil Nadu, southern India.

Etymology. This species is named after the type locality, Kodaikanal (nicknames 'Princess of hill stations'), which is located in upper Palani hills of Tamil Nadu. The epithet is a noun in apposition.

Paramixogaster luxor (Curran, 1931)

Figs 13, 88–94, 132

Microdon luxor Curran, 1931: 306. Holotype ♂: Malaysia (NHMUK) [examined]; Knutson et al. 1975: 371.
Paramixogaster luxor (Curran, 1931) – Reemer and Ståhls 2013a: 145.

Studied type specimens. ***Holotype*** of *Microdon luxor* Curran. Malaysia • 1 ♂; Selangor, Bukit Kutu; 20 Apr. 1926; H.M. Pendlebury leg.; NHMUK. Label 1 (small, round, red-bordered): "Holo- / type"; label 2 (red): "Microdon / Type / luxor [male sign] / Curran / No."; label 3: "Malay Penin: / Selangor, / Bukit Kutu / 3500 ft. / April 20th 1926. / H.M. Pendlebury."; label 4: "Pres. by / Fed. Malay States / Museum / B.M. 1934-74.".

Additional specimens. Malaysia (identification uncertain, see notes) • 1 ♀; SE Sabah, nr. Danum Valley Field C; Malaise trap 7; alt. 150 m.; 20–22 Nov. 1997; C. van Achterberg leg; RMNH (M. Reemer specimen code MR.

Thailand • 1 ♀; Songkhla, Nam Tok Ton Pliu; 17 Feb. 2005; Yanega, D. leg.; UCRC.

Diagnosis. This is the only known Oriental species of *Paramixogaster* in which the scutellum has a pair of apical calcars, and also the only one in which the postpedicel is shorter than the scape. Male genitalia as in Fig. 132.

Redescription (based on holotype). Adult male Body length: 7 mm.

***Head*.** Face occupying ~ 1/4 of head width in frontal view, with sides slightly converging ventrad; black, entirely yellow setulose. Gena narrow, black, yellow setulose. Oral margin laterally slightly produced. Frons and vertex black, yellow setulose. Ocellar triangle not elevated. Occiput black, yellow setulose. Eye bare. Antennal fossa approximately as high as wide. Antenna blackish, except scape brown on basal 4/5; antennal ratio approximately as 4:1:3. Arista slender, slightly more than half the length of postpedicel.

***Thorax*.** Mesoscutum black; short black setulose, except yellow setulose along posterior margin [probably also along transverse suture and possibly along anterior margin, but not visible in type specimen because of grease]. Postpronotum brown, bare. Postalar callus yellowish brown, yellow setulose. Scutellum black; black setulose; with two small apical calcars. Pleurae dark brown. Anepisternum without sulcus; entirely yellow setulose. Anepimeron entirely long yellow setulose. Katepisternum long yellow setulose dorsally; bare ventrally. Katatergite and anatergite short microtrichose. Calypter and halter yellow.

Wing: hyaline; microtrichose, except bare on cell bc, basal 1/3 of cell c, basally on cell r_1 along vein Rs, entirely on cell br (only with microtrichia along vena spuria), on basal 2/3 of cell bm, antero-basal 1/3 of cell cup.

Legs: [Front legs missing in holotype]. Mid leg with femur dark brown on basal 2/3, yellow on apical 1/3; tibia and tarsus yellow; dark setulose on dark parts, yellow setulose on yellow parts. Hind leg with femur dark brown, tibia yellow on basal 2/5 and dark brown on apical 3/5, tarsus yellow; entirely yellow setulose. Coxae and trochanters dark brown; yellow setulose.

***Abdomen*.** Constricted, with narrowest point at anterior margin of tergite 2, widest point at posterior margin of tergite 3. Tergite 1 black; yellow setulose. Tergite 2 black with two large, yellow maculae on anterior 3/4; black setulose, except yellow setulose postero-laterally. Tergites 3 and 4 black [colour of setulae hard to assess in type specimen because of grease, but there seems to be oblique vittae of yellow setulae and a yellow setulose fascia along the posterior margin of tergite 4]. Sternite 1 black; bare. Sternite 2 yellow; yellow setulose. Sternites 3 and 4 black; black setulose. Genitalia as in Fig. 132.

Notes. The studied female from Sabah (Malaysia) possibly belongs to a different species. Usually in Microdontinae, females are wider in body dimensions than males. In this specimen the face and tergite 2 are narrower than in the male holotype. This may indicate that it belongs to a different species. This matter is here left unresolved, because so few specimens are available.

Distribution. Known from Peninsular Malaysia and possibly Sabah.

Paramixogaster sacki **Reemer & Ståhls, 2013**

Figs 21, 95–101, 133

Myxogaster variegata Sack, 1922: 274. Syntypes ♀: Taiwan (type lost?) [not examined].

Paramixogasteroides variegata (Sack, 1922) – Shiraki 1930: 9; Knutson et al. 1975: 374.

Paramixogaster variegata (Sack, 1922) – Reemer and Ståhls 2013a: 145.

Paramixogaster sacki Reemer & Ståhls, 2013a: 145.

Type specimens. *Syntypes* of *Myxogaster variegata* Sack. Taiwan • 2 ♀; Toa Tsui Kutsu; lost [not examined]. ***Neotype*** of *Myxogaster variegata* Sack (new neotype designation, see notes). Taiwan • 1 ♂; Nantou Lienhuachih watershed no. 3; 5 Jun. – 24 Jul. 2006 // C.S. Lin & W.T. Yang leg.; Malaise trap; RMNH. Label 1: “Taiwan Nantou // Lienhuachih // Watershed No: 3 // VI/5–VII/24/2006 // C.S. Lin & W.T. Yang // Malaise trap (KCN)”; label 2: “Paramixogaster // sacki // Det. M. Reemer 2022 // Specimen code MR1391”; label 3 (red): “NEOTYPE // *Myxogaster variegata* // Sack, 1922 // Designated by Reemer & // Sankararaman 2024”.

Additional specimens. Taiwan • 1 ♂; Nantou, Yuanfeng; 13 Aug. – 10 Sep. 2002; C.S. Lin & W.T. Yang leg.; Malaise trap; RMNH • 1 ♂; Nantou, Lienhuachih Watershed No: 3; 5 Jun. – 24 Jul. 2006; C.S. Lin & W.T. Yang leg.; Malaise trap; RMNH.

Diagnosis. Body length: male 9–12 mm (*n* = 3); female 10 mm (Sack 1922). This species differs from all other known species of *Paramixogaster* by its unique colour pattern: the mesoscutum is largely yellow, with small two black maculae posterior to the postpronotum and two elongate narrow black maculae between the transverse suture and the posterior margin (Fig. 21). Tergites 3 and 4 are yellow with a unique pattern of black vittae (Fig. 95). Male genitalia as in Fig. 133.

Notes. Sack (1922) described *Myxogaster variegata* based on two female syntypes. Attempts to locate the types at the German institutions DEI and ZMHU were unsuccessful (Eliana Buenaventura, Sven Marotzke, Frank Menzel and Joachim Ziegler pers. comm. 2020). The syntypes are considered to be lost. However, the description and figure by Sack (1922) provide enough information to identify the studied specimens as this species. We designate here a neotype to ensure the proper and consistent interpretation of the name.

Shiraki (1930) found out that this species is not closely related to the New World genus *Mixogaster* Macquart, 1842 and erected a new genus for it: *Paramixogasteroides* Shiraki, 1930. He also gave a redescription of the species based on a male and a female. *Paramixogasteroides* was synonymised with *Paramixogaster* by Cheng and Thompson (2008), which was followed by Reemer and Ståhls (2013a) and in this paper.

Distribution. Taiwan.

Paramixogaster sulawesiana Reemer, sp. nov.

https://zoobank.org/CA474375-C39E-4B84-A415-AFE8516003C2
Figs 12, 102–108, 134

Type material. ***Holotype*.** Indonesia • 1 ♂; Sulawesi, Rantepao; July 1936; leg. L.J. toxopeus; coll. RMNH. Label 1: "C. [handwritten, printed letters SW are crossed out] Celebes // VII // Rantepao. // L.J. Toxopeus 1936"; label 2: "Paramixogaster // sp. n. // Det. M. Reemer 2021 // Specimen MR1392"; label 3 (red): "HOLOTYPE // Paramixogaster // sulawesiana // Reemer 2024".

***Paratypes*.** Indonesia • 1 ♂ 1 ♀; Sulawesi, coll. USNM. [specimen labels only state "Macassar"; [unique specimen identifiers USNMENT01541879 and USNMENT01541880 for male and female, respectively].

Diagnosis. Body length: 8–9.5 mm. Belongs to the group of species with lateral bulges on the frons (Figs 104, 105, 107). From *P. fujianensis* it differs by tergite 2 being less than twice as long as wide (more than twice as long as wide in *P. fujianensis*). From *P. icariiformis* it differs by the presence of fasciae of golden setulae along the posterior margins of tergites 3 and 4 (absent in *P. icariiformis*). There is a continuous fascia of golden setulae along the transverse suture of the scutum, and there are fasciae of golden setulae along the posterior margins of tergites 3 and 4 (Fig. 102). These fasciae are not as dense and as sharply demarcated as in *P. kodaiana* Sankararaman & Reemer, sp. nov. (from which it also differs by the lack of dark colouration in wing cell r_{4+5}), but more similar to those in *P. huoi* Reemer, nom. nov. From the latter species, *P. sulawesiana* Reemer, sp. nov. differs by the wing venation: the apex of R_{2+3} is situated well beyond the joint of M_1 with R_{4+5} (at approximately the same level in *P. huoi* Reemer, nom. nov.). Male genitalia as in Fig. 134.

Description (based on holotype). Adult male. Body length: 9 mm.

***Head*.** Face occupying ~ 1/2 of head width in frontal view, with sides somewhat converging ventrad; blackish brown with widely yellow lateral and ventral margins; entirely golden yellow setulose. Gena yellow, yellow setulose. Oral margin not notched anteriorly, laterally weakly produced. Frons posteriorly with shining blackish pair of lateral bulges which are short black setulose, except golden yellow setulose on a triangular patch adjacent to eye margin, these bulges are separated by a narrow yellowish crease; frons anteriorly (laterad of antennal fossa) with pair of more or less flat yellow areas which are golden yellow setulose, separated from face by pair of shiny black bare maculae. Vertex swollen, with oblique depressions converging anteriad; blackish brown; short black setulose except golden yellow setulose along all margins. Occiput black;

golden yellow setulose dorsally, white setulose ventrally. Eye bare. Antennal fossa approximately as high as wide. Antenna orange-brown; postpedicel 6.5× as long as scape. Arista ~ 2× as long as scape.

***Thorax*.** Mesoscutum blackish brown; short black setulose, except for narrow fascia of golden yellow setulae along transverse suture, large patch of golden yellow setulae anterior to scutellum, and small patch of golden yellow setulae anterior to postalar callus. Postpronotum brown, bare. Postalar callus yellow, golden yellow setulose. Scutellum without calcars; yellow; golden yellow setulose. Pleura yellowish dorsally, brown ventrally. Anepisternum and anepimeron entirely covered with thick golden yellow setulae, appressed and directed hindward. Katepisternum long golden yellow setulose dorsally; bare ventrally. Katepimeron with a few long yellow setulae. Katatergite and anatergite short microtrichose. Metanotum shining brown. Calypter and halter yellow.

Wing: hyaline; microtrichose, except bare in cell r_1 narrowly along Rs, narrowly along veins in basal 1/3 of r_{4+5}, entirely on cell br (except for microtrichia along vena spuria), narrowly along veins in antero-basal 1/5 of cell dm, entirely on cell bm, basal 2/3 of cell cup.

Legs: yellowish brown, except hind femur darker brown.

***Abdomen*.** Constricted basally, narrowest at basal 1/6 of tergite 2, widest at transition between tergites 3 and 4. Tergite 1 dark brown; yellowish setulose. Tergite 2 dark brown with two large, elongate, pale yellow maculae from anterior margin to ~ 3/5 of tergite, and yellow fascia of ~ 1/6 of tergal length along posterior margin; short black setulose, except bare on yellow maculae with fascia of thick golden yellow setulae along posterior margin. Tergite 3 dark brown, except yellowish brown fascia of ~ 1/5 of tergal length along posterior margin; black setulose anteriorly, golden yellow setulose posteriorly. Tergite 4 dark brown except widely yellow along posterior and lateral margins; short black setulose antero-medially, golden yellow setulose postero-medially and laterally. Sternite 1 brown; sparsely short black setulose. Sternite 2 yellow; bare. Sternites 3 and 4 brown; yellow setulose. Genitalia as in Fig. 134.

Notes. The male paratype differs from the holotype in the following aspects: body length 8.5 mm; postpedicel 8× as long as scape; vertex golden yellow setulose; dark parts on head, thorax, and abdomen more brownish (rather than blackish as in holotype). The female paratype (in which the antennae are missing) differs from the male holotype in the same aspects of colouration, as well in the body length of 9 mm. The colour differences between holotype and paratype are considered to either represent intraspecific variation or result from differences in preservation history.

Distribution. Only known from Sulawesi (Indonesia).

Etymology. The specific epithet (adjective) refers to the type locality.

Paramixogaster vespiformis (de Meijere, 1908)

Figs 46–53, 117–122, 137

Microdon vespiformis de Meijere, 1908: 210. Lectotype ♀: Indonesia, Java (RMNH) [examined]; Knutson et al. 1975: 372.

Paramicrodon decipiens de Meijere, 1917: 242. Holotype ♀: Indonesia, Java (RMNH) [examined].

Paramicrodon dicipiens de Meijere, 1917 – Knutson et al. 1975: 373 (misspelling).
Paramixogaster decipiens (de Meijere, 1917) – Reemer and Ståhls 2013a: 145.
Paramixogaster vespiformis (de Meijere, 1908) – Reemer and Ståhls 2013a: 145.

Studied type specimens. ***Lectotype*** of *Microdon vespiformis* de Meijere (designated here, see notes). Indonesia • 1 ♀; label 1: "E. Jacobson Batavia Sept. 1907"; label 2: "*Microdon vespiformis* type det. de Meijere"; label 3 (red): "*Microdon vespiformis* de Meijere, 1908 ZMAN type DIPT.1074.1"; RMNH.

Indonesia • 1 ♀, paralectotype (new designation, see notes) of *Microdon vespiformis* de Meijere; label 1: "*Microdon vespiformis*"; label 2: "*Microdon vespiformis* de Meijere, 1908 ZMAN type? DIPT.1074"; RMNH.

Holotype of *Paramicrodon decipiens* de Meijere. Indonesia • 1 ♀; Java; RMNH. Label 1: "Salatiga V.1915 Roepke"; label 2: "*Paramicrodon decipiens* det. de Meijere Type"; label 3 (red): "Microdon decipiens de Meijere, 1917 ZMAN type DIPT.0975.1"; RMNH.

Paratypes of *Paramicrodon decipiens* de Meijere (only puparia, no adult specimens, although probably the holotype was reared from one of these specimens). Indonesia • 3 empty puparia on a piece of dry leaf. Label 1: "Salatiga V.1915 Roepke"; label 2: "*Paramicrodon decipiens* de Meijere, 1917 ZMAN type? DIPT.0975".

Additional specimens. Indonesia • 1 ♀; Java; Apr. 1908; E. Jacobson leg.; RMNH • 1 ♀; Java, Dungus Iwul; 2 Dec. 1952; alt. 100 m; M.A. Lieftinck leg.; RMNH • 3 ♂ 1 ♀; Sumatra, Fort De Kock; alt. 920 m; 1925; E. Jacobson leg.; RMNH • 1 ♀; W. Bali, nr. Negara, rainforest above Batuagung; alt. 550 m; 4–6 Dec. 1991; C. van Achterberg leg.; RMNH.

Malaysia • 1 ♂; Penang; 1927; C.F. Baker leg.; USNM • 1 ♂; Penang; 8 Dec. 1942; H.T. Pagden leg.; NHMUK [13933416].

Philippines • 1 ♂; Palawan, Brookes, Point Uring Uring; 16 Aug. 1961; Noona Dan. Exp. 61–62 leg.; ZMUC • 1 ♂; Palawan, Brookes, Point Uring Uring; 10 Sep. 1961; Noona Dan. Exp. 61–62 leg.; ZMUC • 1 ♂; Palawan, Mantalingajan, Pinigisan; 7 Sep. 1961; Noona Dan. Exp. 61–62 leg.; ZMUC • 1 ♂; Balabac, Dalawan Bay; 8 Oct. 1961; Noona Dan. Exp. 61–62 leg.; ZMUC • 1 ♂; Balabac, Dalawan Bay; 13 Oct. 1961; Noona Dan. Exp. 61–62 leg.; ZMUC • 1 ♀; Balabac, Dalawan Bay; 10 Oct. 1961; Noona Dan. Exp. 61–62 leg.; ZMUC.

Thailand • 1 ♀; Chantaburi Prov., Tha Mai District, Ao Khating; 1 Jan. 1992; G.R. Ballmer leg.; UCRC [label: "Photo KC64-318:31-33"]

Diagnosis. Body length: males 7–9 mm (*n* = 7), females 6–10 mm (*n* = 6). This belongs to the group of species without lateral bulges on the frons. From *P. luxor* it differs by the postpedicel being longer than the scape (shorter in *P. luxor*). From *P. contracta* and *P. conveniens* it differs by the incomplete transverse suture (complete in *P. contracta* and *P. conveniens*). From *P. sacki* it differs by tergites 3 and 4 being black with yellow posterior margin (yellow with pattern of black vittae in *P. sacki*). It differs from *P. jubata* Reemer, sp. nov. by the shorter tergite 2, of which the posterior margin is wider than the median length (longer in *P. jubata* Reemer, sp. nov.), the dark anterior margin of the scutellum (entirely yellow in *P. jubata* Reemer, sp. nov.) and the shorter setulae on the vertex.

Paramixogaster vespiformis is most similar to *P. indica*, from which it differs by the interrupted yellow vitta between postpronotum and posterior callus (continuous in *P. indica*), and the shorter postpedicel in the male, which is 3.3–3.7× as long as the scape (4.4–5.6× as long in *P. indica*). Male: postpedicel

3.3–3.7× as long as scape. Female: postpedicel 1.6–2.9× as long as scape. The degree of infuscation of wing apex is very variable. Male genitalia as in Fig. 137.

Notes. The description of *Microdon vespiformis* by de Meijere (1908) was based on an unknown number of specimens. The specimen identified as syntype by de Jong (2000) is clearly a primary type, based on the label information and the concurrence of its characters with the original description. This specimen is here designated as lectotype. The RMNH collection also holds a female specimen which is considered by de Jong (2000) as a possible syntype of *Microdon vespiformis* de Meijere. The label is in de Meijere's handwriting and the specimen agrees well with the other syntype, except that it is smaller (6 mm), and it has a peculiar forked appendix on vein R_{4+5}. This latter character is considered as an abnormality. Unlike the lectotype, however, this specimen has no locality information on the label. Besides, de Meijere (1908) does not mention a smaller specimen with an aberrant wing venation. Therefore, this specimen is here regarded as not belonging to the type series.

In the same paper as the one in which he described *Microdon vespiformis*, de Meijere (1908) also described specimens from Bali which he identified as *Microdon indicus* (Doleschall). However, as de Meijere noted himself, these specimens differ from *M. indicus* as described by Doleschall (1857), and also from *Microdon vespiformis* de Meijere, 1908, because the frons is rather uneven ('ziemlich uneben') and bears two large, round elevations ('etwas erhabenen grossen runden Stellen'). This character reminds of the lateral bulges on the frons found in several other *Paramixogaster* species (e.g., *P. icariiformis*, *P. sulawesiana* Reemer, sp. nov., Fig. 6), but not in *P. indica* or *P. vespiformis*. Probably, the Balinese specimens referred to by de Meijere as *C. indica* were misidentified. Unfortunately, no specimens identified by de Meijere as *C. indica* could be found in the collection of the RMNH (which nowadays includes the collection of the former ZMAN, in which most of de Meijere's material was deposited). So, the identity of *Microdon indicus* (Doleschall) *sensu* de Meijere (1908) remains unclear.

The empty puparia (Figs 52, 53) listed among the type specimens of *Paramicrodon decipiens* de Meijere have also been described by de Meijere (1917), so these can be regarded to belong to the type series (de Jong 2000). As the species description is based on the single adult female, thus the holotype, the empty puparia are considered paratypes.

In the holotype of *P. decipiens* there is no appendix on vein R_{4+5}. Otherwise, the species is very similar to the other specimens here identified as *P. vespiformis*. In some of the specimens from the Philippines this appendix is also lacking, whereas in one specimen it is only present in one of the wings.

Paramixogaster vespiformis is very similar to *P. indica*, so such an extent that these taxa might be considered synonymous as well in the future. Unfortunately, most of the available specimens are at least several decades old, so molecular analyses are not very feasible. As the morphological differences are small, but consistent, here the view is taken that these taxa represent two different, albeit closely similar species.

The separation between the ranges of *P. indica* and *P. vespiformis* seems to follow the line of Wallace, as well as Huxley's adaptation of it (Lohman et al. 2011), with *P. indica* being the Wallacean species and *P. vespiformis* occurring on the Sunda Shelf. The single exception seems to be a female specimen from Bali (collected near Negara rainforest, above Batuagung, 4–6.XII.1991, leg. C. van Achterberg, coll. RMNH). The yellow lateral vitta along the scutum is continuous in this specimen, which would indicate *P. indica*. However, the other characters differentiating between *P. indica* and *P. vespiformis* can only be seen in males, so identification based on this single colour character remains a bit uncertain. This female specimen is here left unidentified and it is therefore not listed among the studied specimens. It would not be the first 'Wallacean' taxon to colonise Bali (Tänzler et al. 2014), but more specimens are needed to confirm that this is indeed the case.

A larva of this species was found by Greg R. Ballmer (pers. comm. 2023) in Thailand in 1992 in a folded leaf shelter, also occupied by ants, putative *Dolichoderus thoracicus* (Smith, 1860) (Fig. 4). This specimen was reared to the adult stage, and the adult specimen is mounted together with the empty puparium. See section *Additional material* for further details.

Distribution. Known from Thailand, Peninsular Malaysia, the Indonesian islands Sumatra, Java and Bali, and the Philippines. From the Philippines, all specimens are from the islands Balabac and Palawan. All known localities are situated west of the Wallace Line (and also of Huxley's adaptation of it).

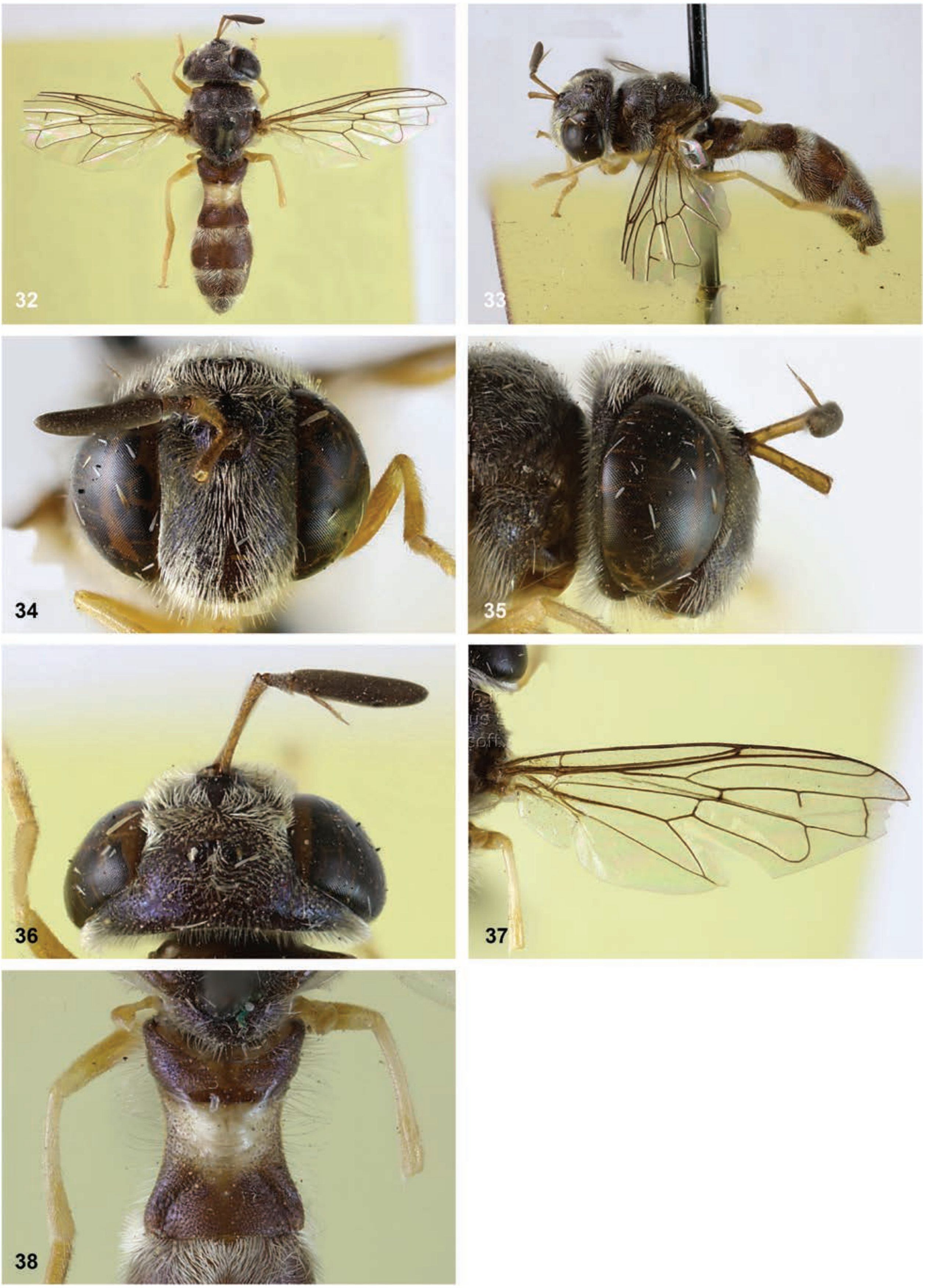
Paramixogaster yunnanensis Cheng in Huang & Cheng, 2012

Paramixogaster yunnanensis Cheng in Huang & Cheng, 2012: 696. Holotype ♂: China, Yunnan (CASB, but see notes) [not examined]; Reemer and Ståhls 2013a: 145.

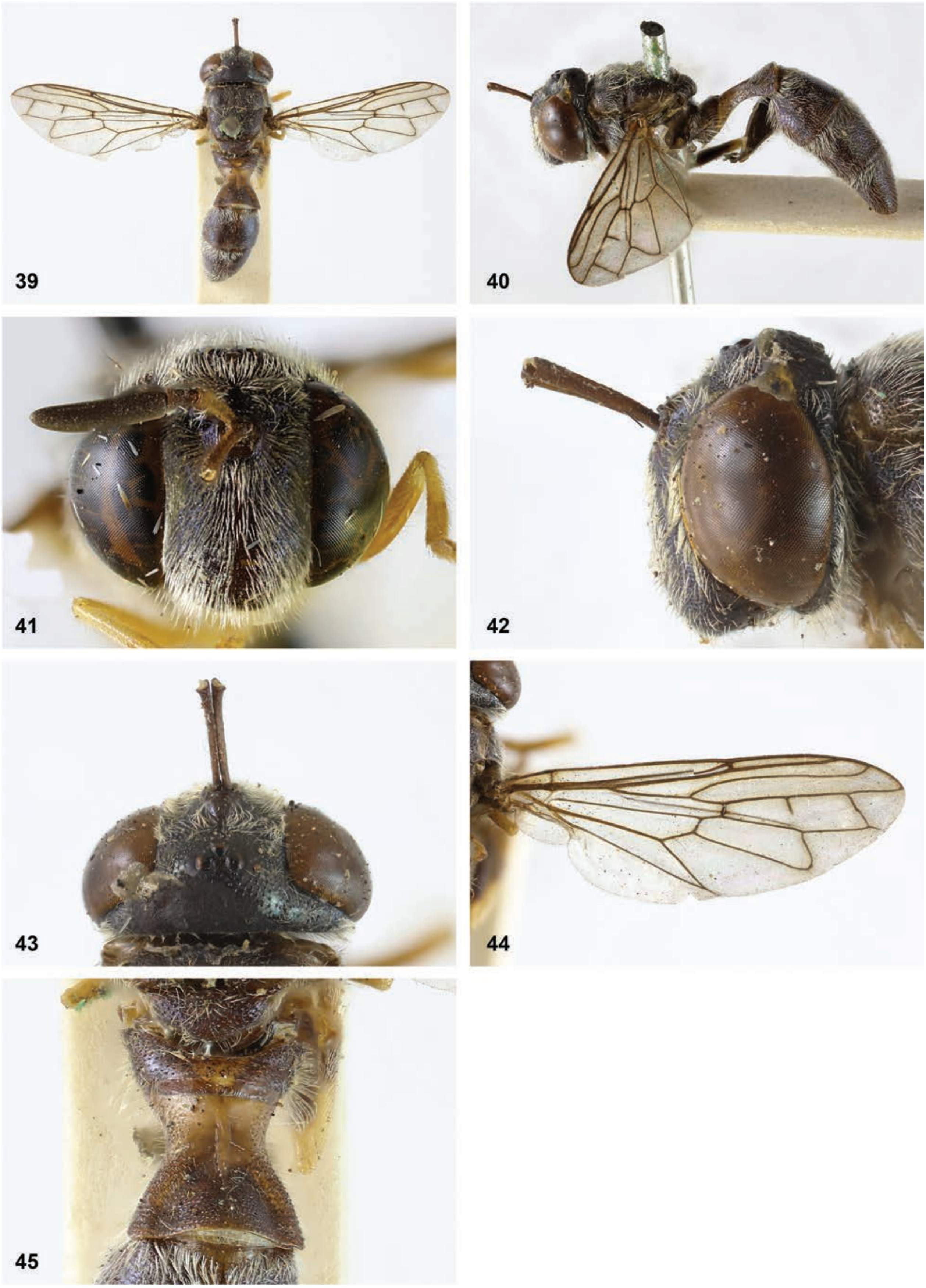
Diagnosis. Only male known. Body length: 7 mm. This belongs to the group of species with lateral bulges on the frons. From *P. fujianensis* it differs in tergite 2 being less than twice as long as wide (more than twice as long as wide in *P. fujianensis*). From *P. icariiformis*, *P. kodaiana* Sankararaman & Reemer, sp. nov., *P. huoi* Reemer, nom. nov. and *P. sulawesiana* Reemer, sp. nov. it differs by the absence of a fascia of golden setulae along the transverse suture of the scutum (present in the four aforementioned species). From *P. brunettii* it differs by the black tergite 2 (reddish in *P. brunettii*) with a pair of yellow maculae. From *P. halmaherensis* Reemer, sp. nov. it differs by the dark postalar calli (yellow in *P. halmaherensis* Reemer, sp. nov.), the longer postpedicel, which is 8× as long as scape (6× as long in *P. halmaherensis* Reemer, sp. nov.), and the entirely clear wing (infuscate in apical 1/2 of cells r_1 and r_{2+3} in *P. halmaherensis* Reemer, sp. nov.). Figures of habitus and head are provided by Huang and Cheng (2012). Note that these characters are based on the description only and could not be verified against any specimens.

Notes. Unsuccessful attempts were made to locate the type specimen of *Paramixogaster yunnanensis* by trying to contact the author and by enquiring at the CASB collection (Ke-Ke Huo pers. comm. 2023). The original description in Huang and Cheng (2012) is in Chinese, but the same work also provides an English translation, as well as figures of the head in frontal view and of the thorax and abdomen in dorsal view. This information suggests that *P. yunnanensis* is very similar to *P. halmaherensis* Reemer, sp. nov.

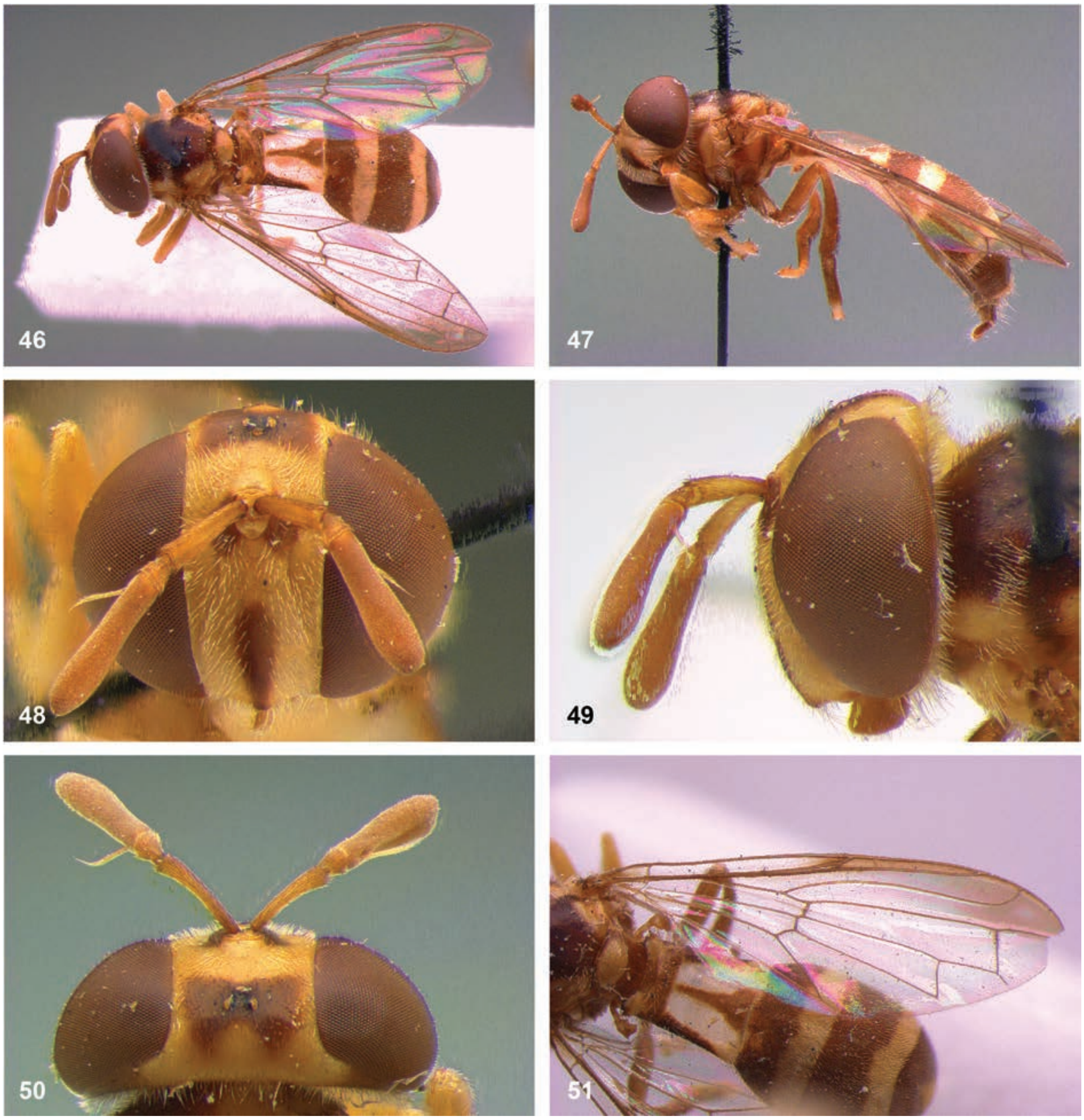
Figures 29–31. *Paramixogaster brunettii* Reemer, holotype: **29** mounted specimen and labels **30** habitus dorsolateral **31** head and thorax dorsolateral. Photos by J. van Steenis.



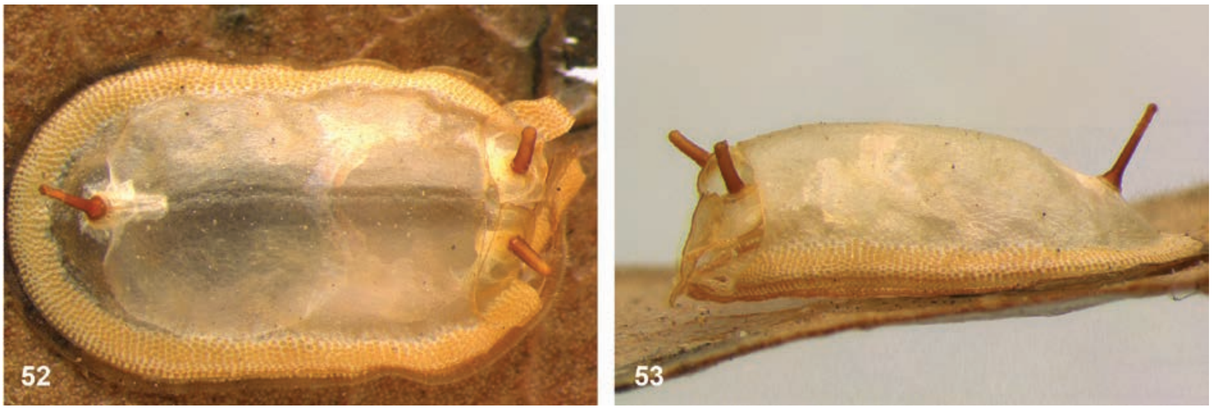
Figures 32–38. *Paramixogaster contracta* (Brunetti), female, holotype: **32** habitus, dorsal **33** habitus, lateral **34** head, frontal **35** head, lateral **36** head, dorsal **37** wing **38** tergite 2, dorsal.



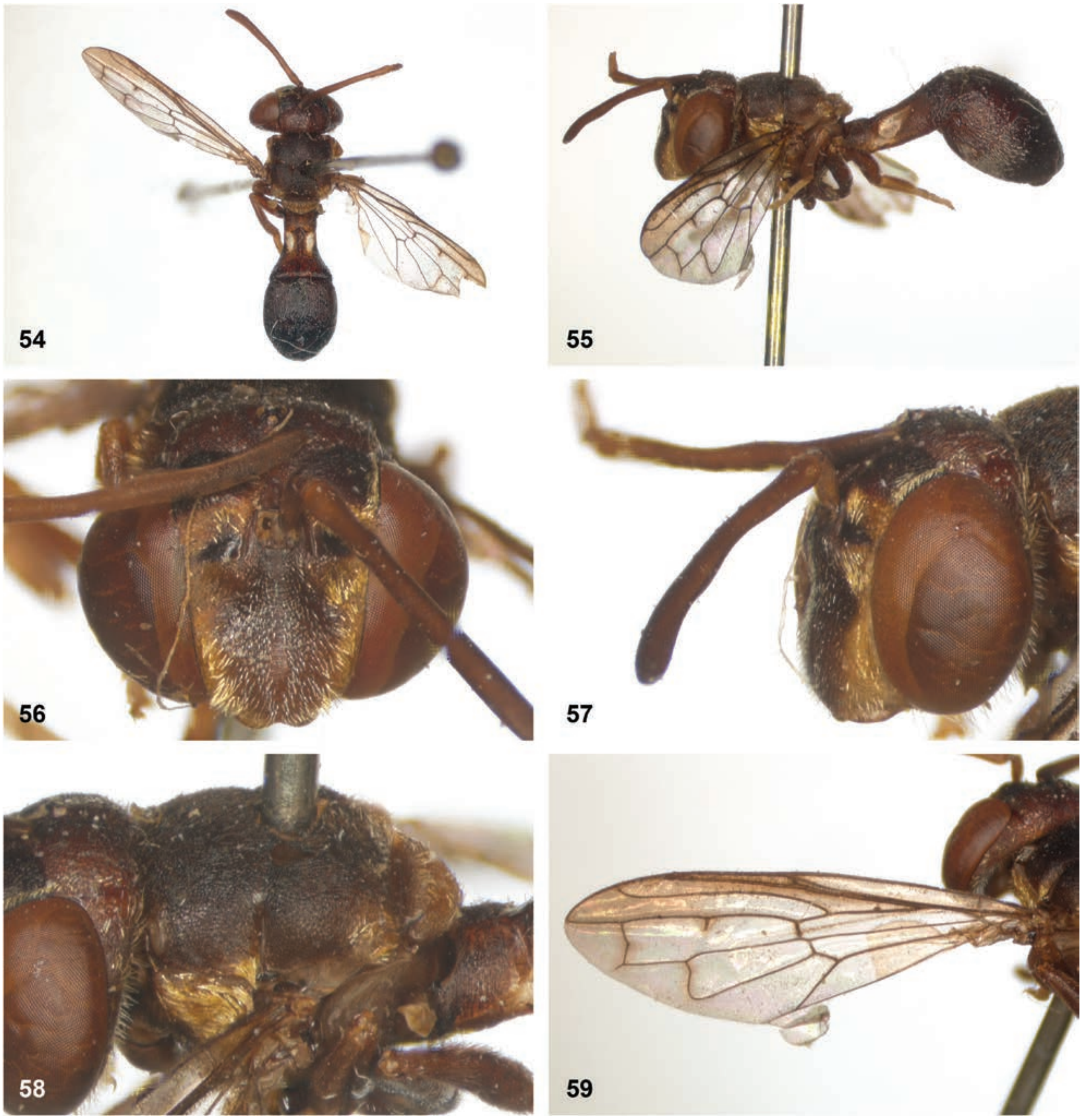
Figures 39–45. *Microdon conveniens* Brunetti, female, holotype: **39** habitus, dorsal **40** habitus, lateral **41** head, frontal **42** head, lateral **43** head, dorsal **44** wing **45** tergite 2, dorsal.



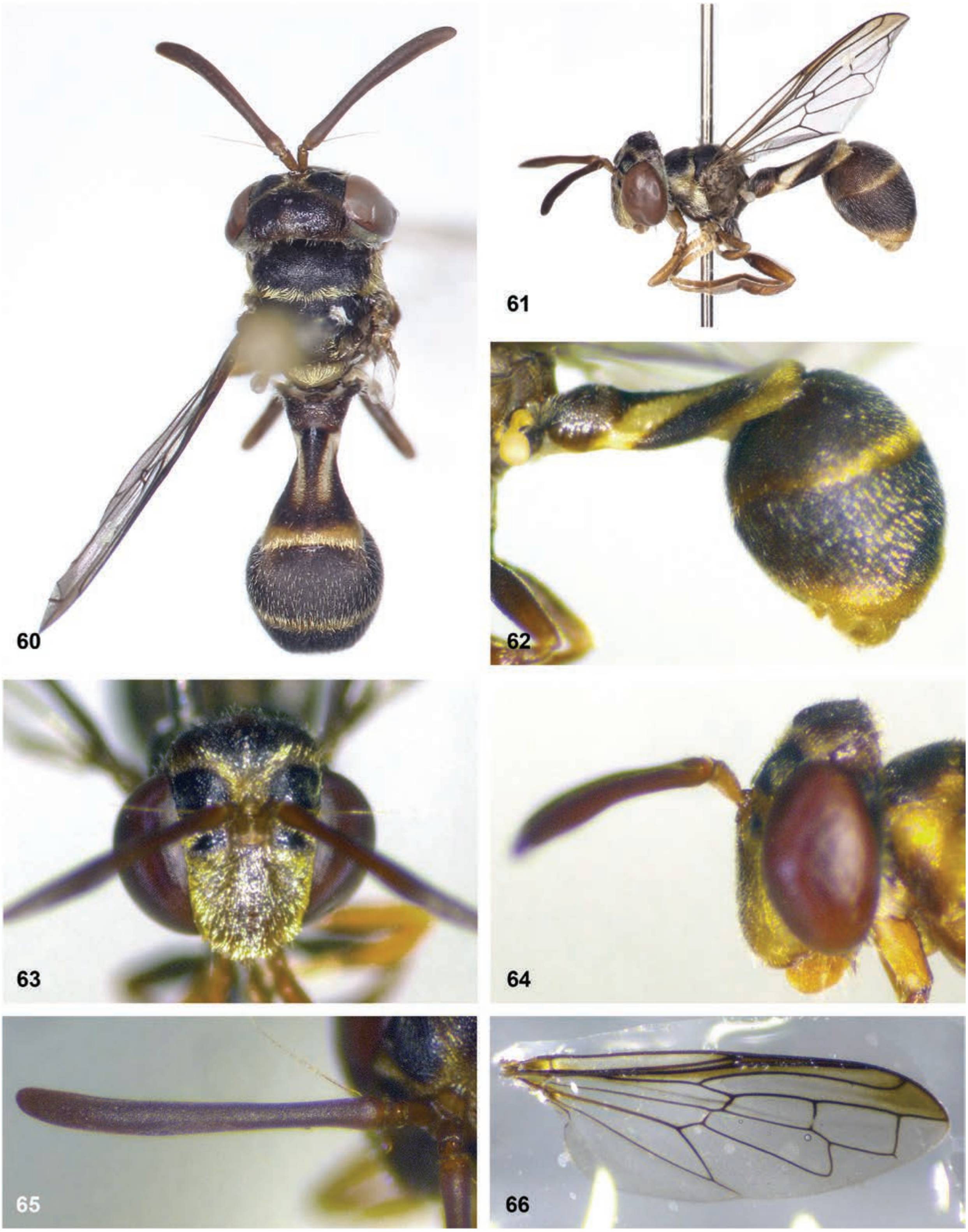
Figures 46–51. *Microdon decipiens* de Meijere, female, holotype: **46** habitus, dorsal **47** habitus, lateral **48** head, frontal **49** head, lateral **50** head, dorsal **51** wing.



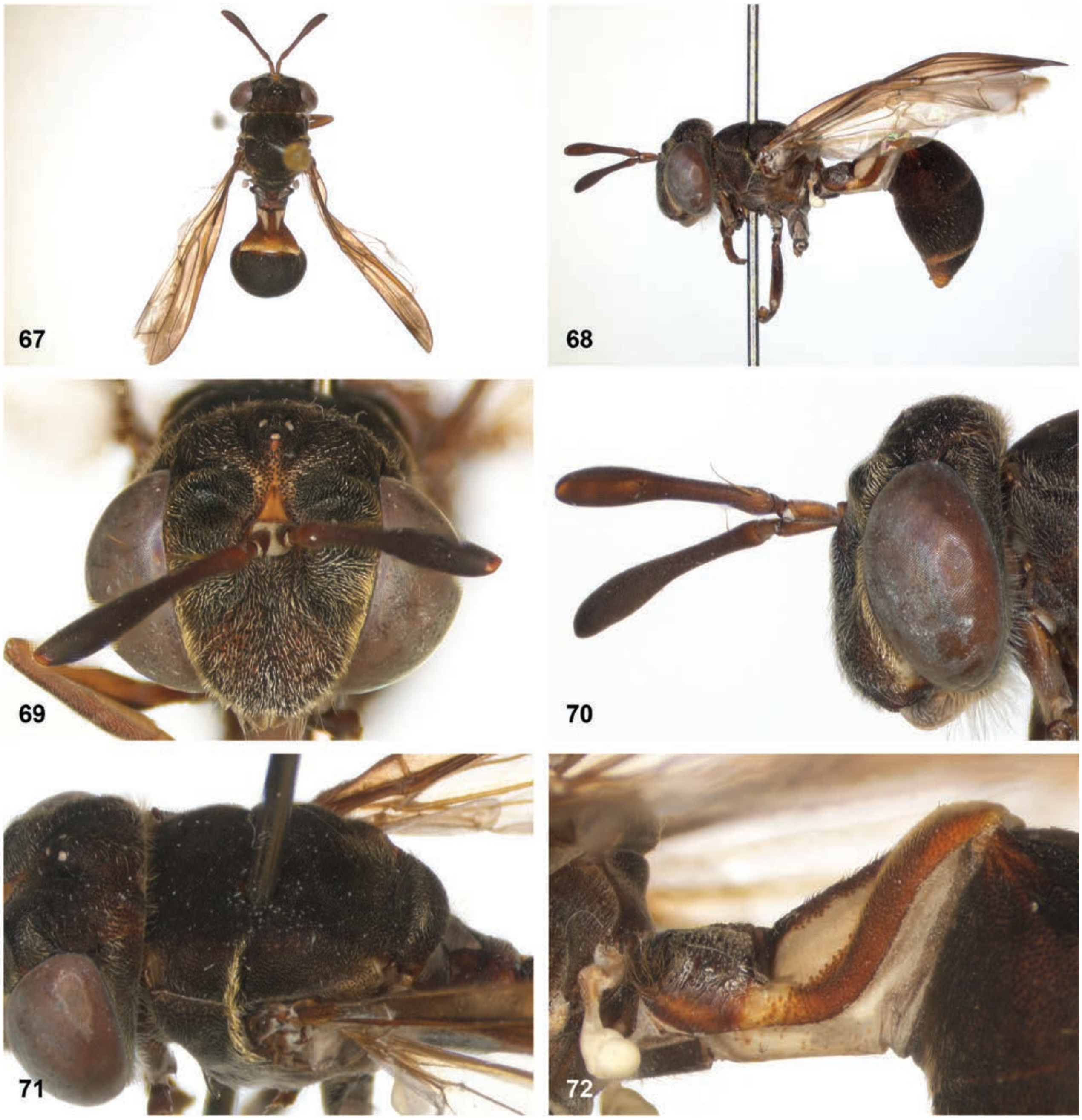
Figures 52, 53. *Microdon decipiens* de Meijere, puparium, paratype: **52** habitus, dorsal **53** habitus, lateral.



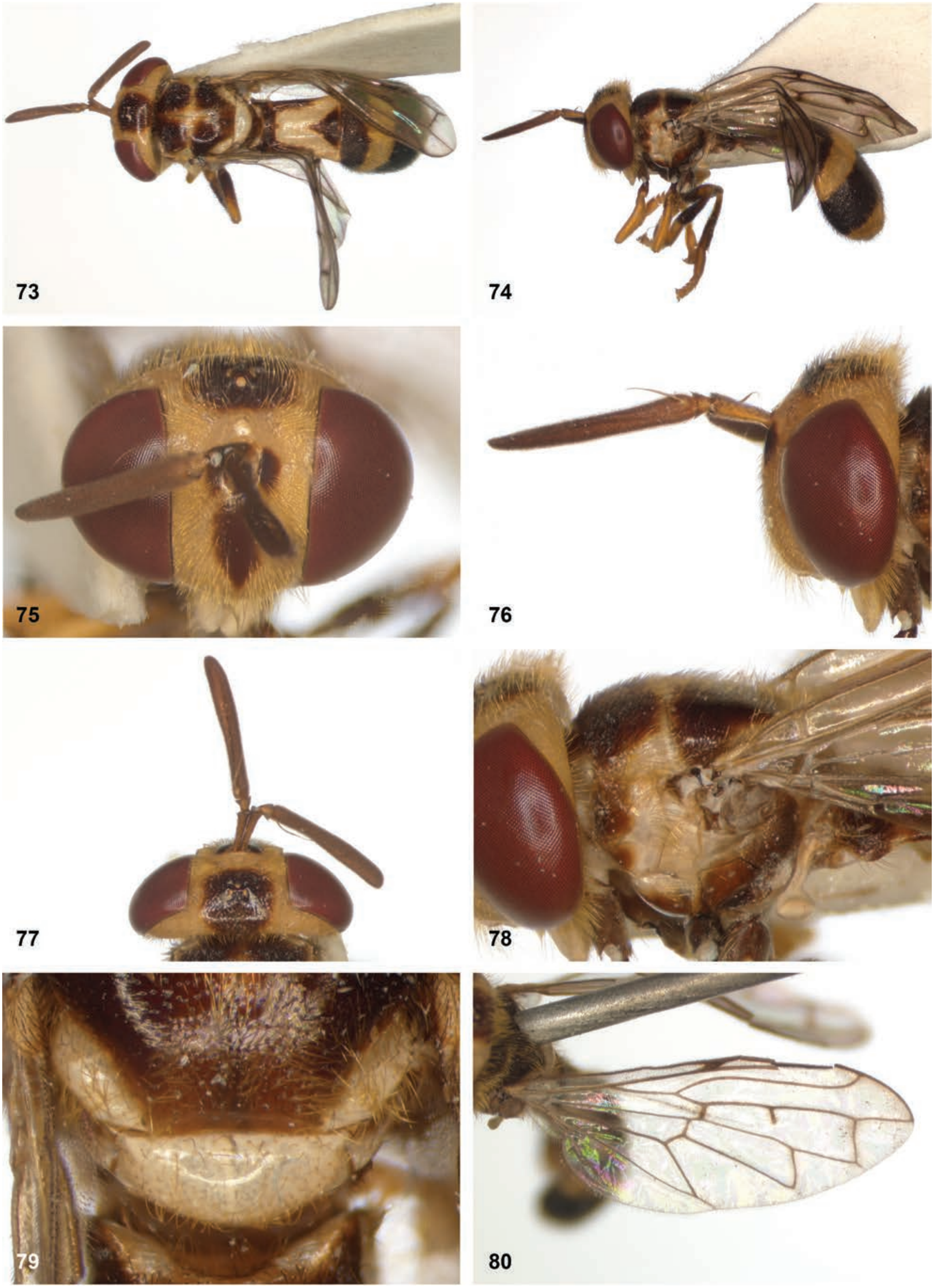
Figures 54–59. *Paramixogaster halmaherensis* Reemer, sp. nov. male, holotype: **54** habitus, dorsal **55** habitus, lateral **56** head, frontal **57** head, fronto-lateral **58** thorax, dorso-lateral **59** wing.



Figures 60–66. *Paramixogaster huoi* Reemer, nom. nov. male, holotype: **60** habitus, dorsal **61** habitus, lateral **62** abdomen, lateral **63** head, frontal **64** head, lateral **65** antenna **66** wing.

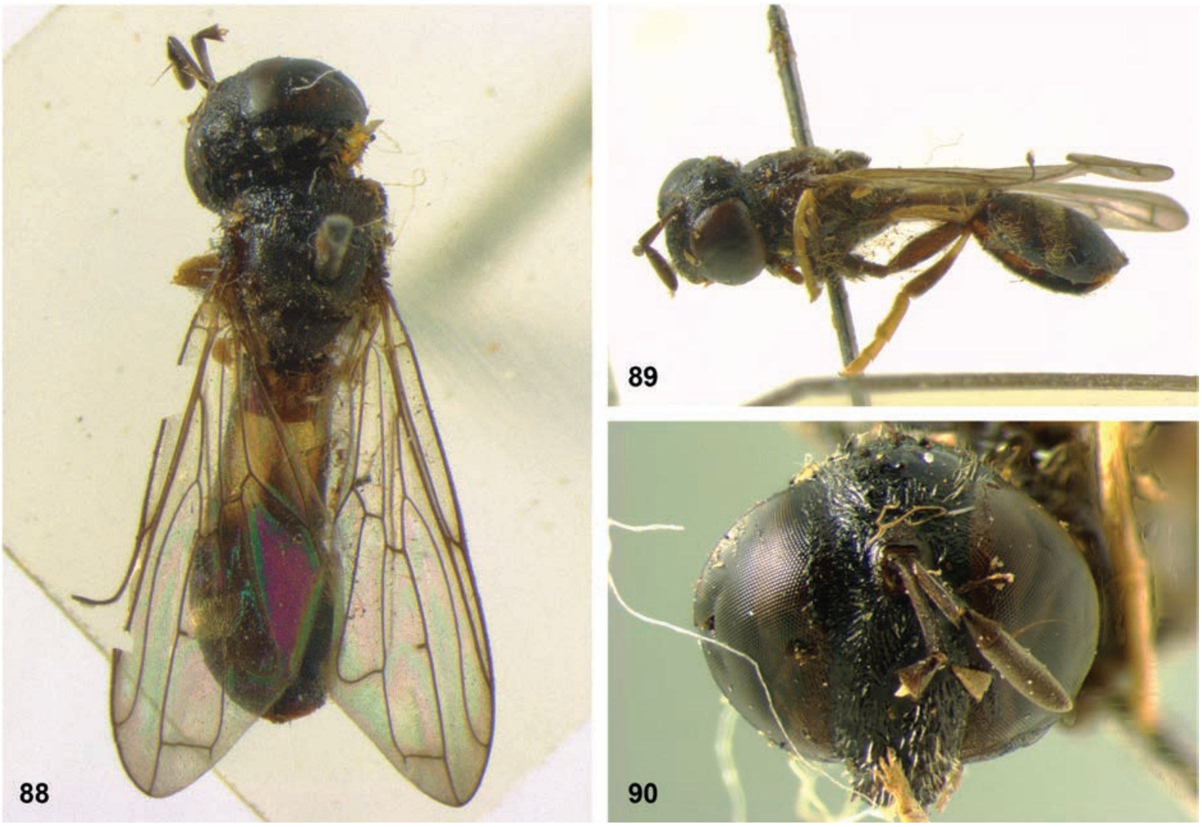


Figures 67–72. *Paramixogaster icariiformis* Pendlebury female, neotype: **67** habitus, dorsal **68** habitus, lateral **69** head, frontal **70** head, lateral **71** thorax, dorso-lateral **72** tergite 2, lateral.



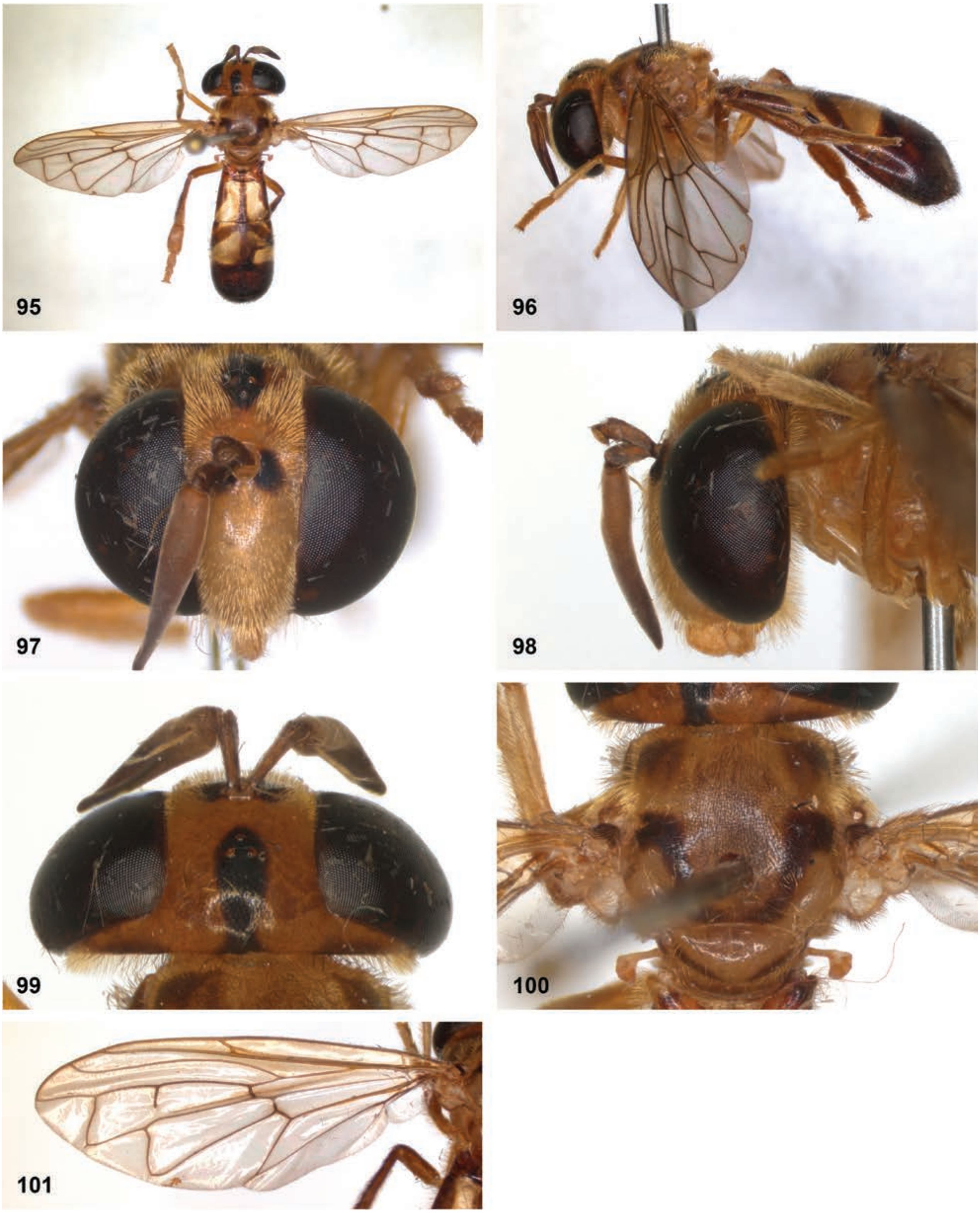
Figures 73–80. *Paramixogaster jubata* sp. nov. male, holotype: **73** habitus, dorsal **74** habitus, lateral **75** head, frontal **76** head, lateral **77** head, dorsal **78** thorax, lateral **79** scutellum, dorsal **80** wing.

Figures 81–87. *Paramixogaster kodaiana* Sankararaman & Reemer, sp. nov. female, holotype: **81** habitus, dorsal **82** habitus, lateral **83** head, frontal **84** head, dorsal **85** tergite 2, dorsal **86** thorax, dorsal **87** wing.

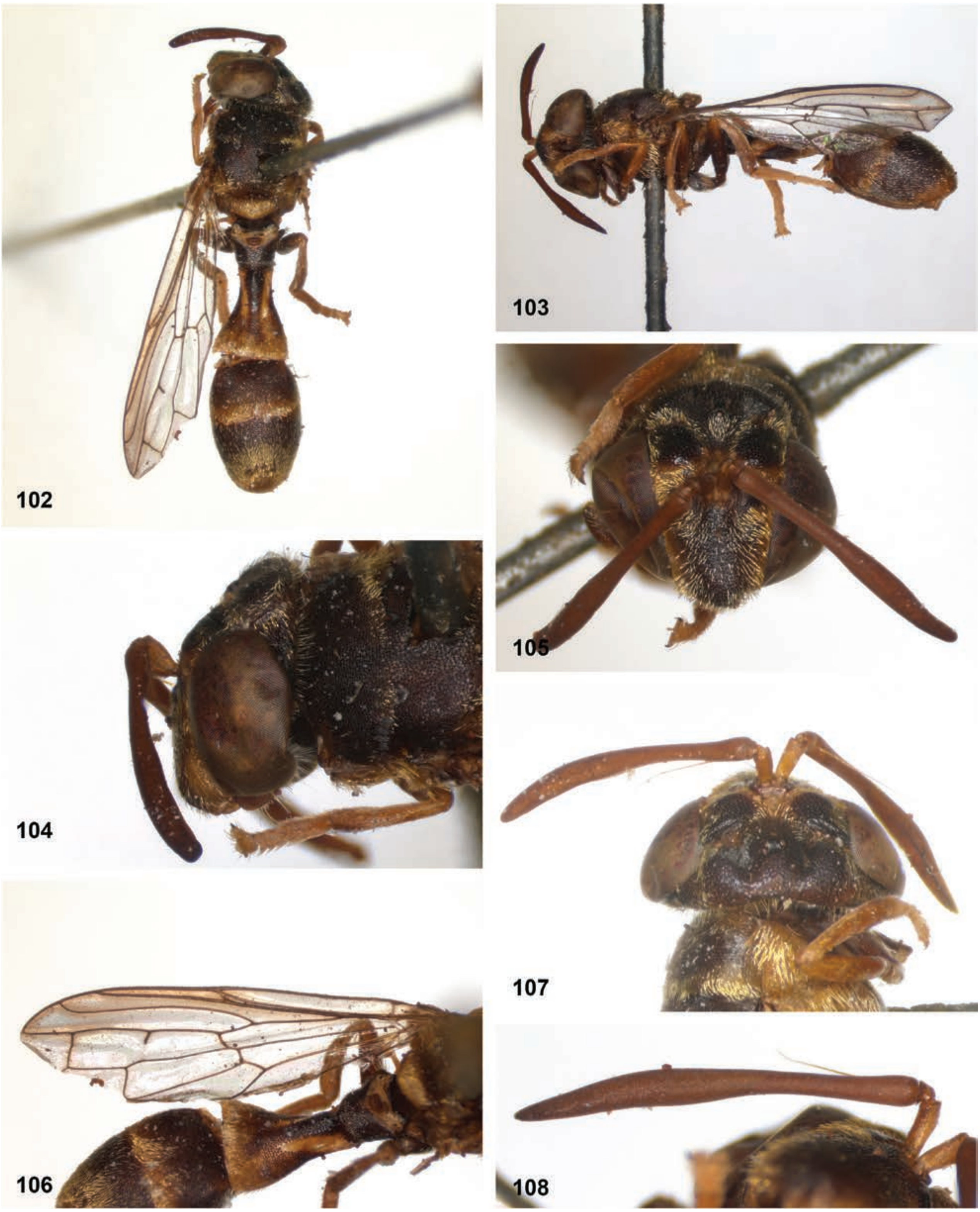


Figures 88–90. *Microdon luxor* Curran male, holotype: **88** habitus, dorsal **89** habitus, lateral **90** head, frontal.

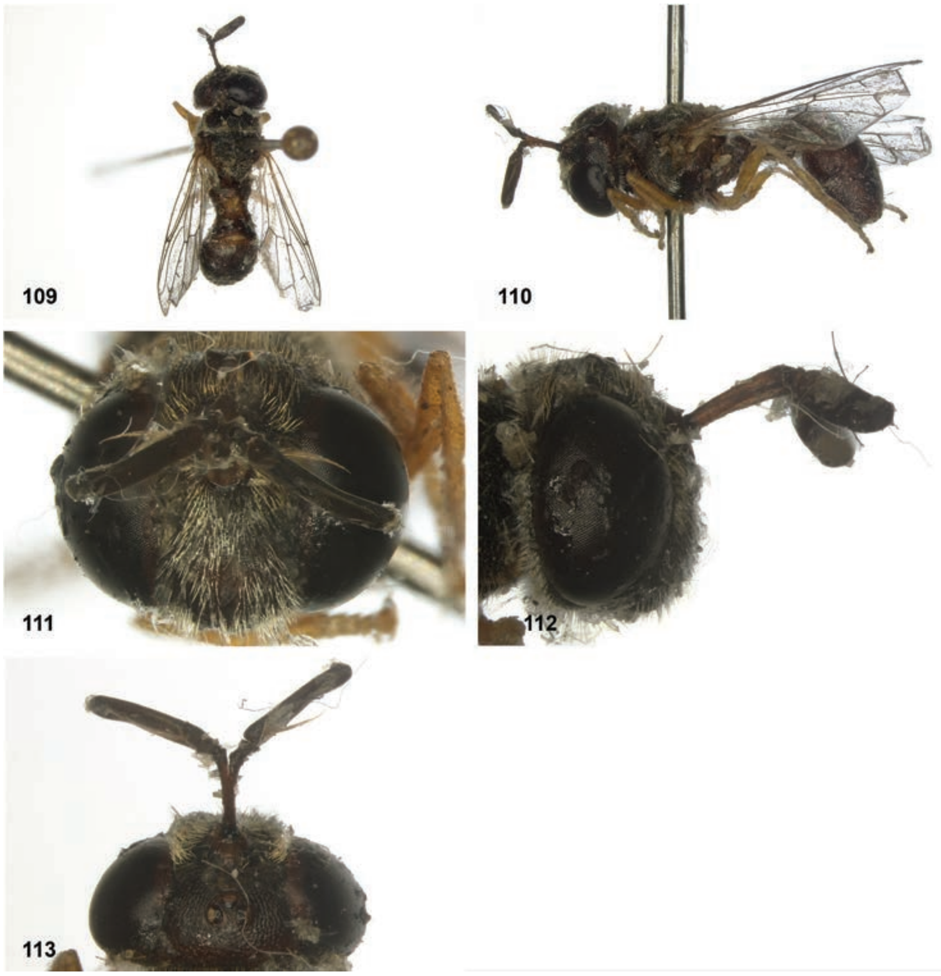
Figures 91–94. *Paramixogaster* cf. *luxor* (Curran) female, Sabah: **91** habitus, dorsal **92** habitus, lateral **93** head, dorsal **94** head, frontal.



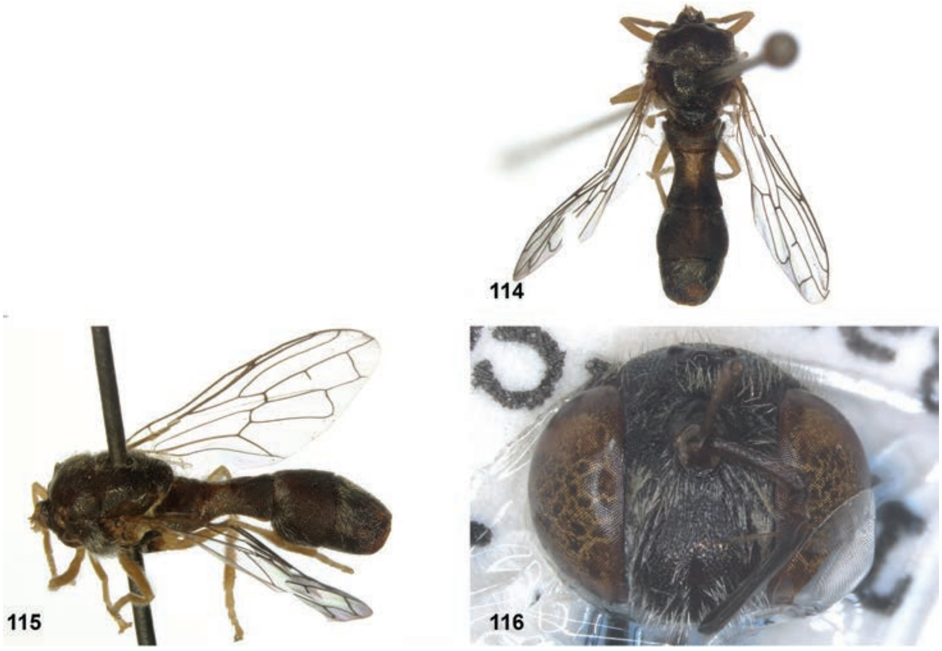
Figures 95–101. *Paramixogaster sacki* Reemer & Ståhls male, neotype: **95** habitus, dorsal **96** habitus, lateral **97** head, frontal **98** head, lateral **99** head, dorsal **100** thorax, dorsal **101** wing.



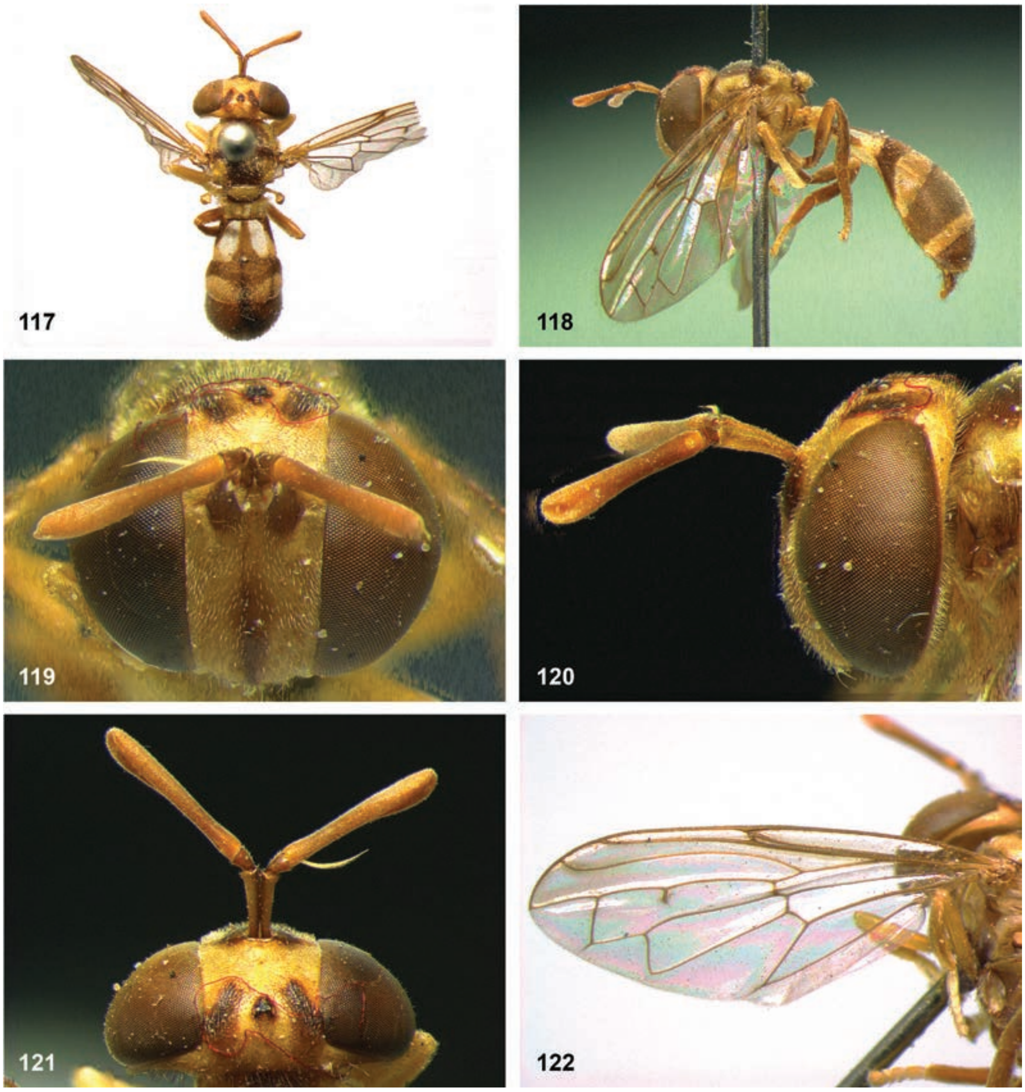
Figures 102–108. *Paramixogaster sulawesiana* sp. nov. male, holotype: **102** habitus, dorsal **103** habitus, lateral **104** head, lateral **105** head, frontal **106** wing **107** head, dorsal **108** antenna.



Figures 109–113. *Microdon subpetiolatus* Thompson male, holotype: **109** habitus, dorsal **110** habitus, lateral **111** head, frontal **112** head, lateral **113** head, dorsal.

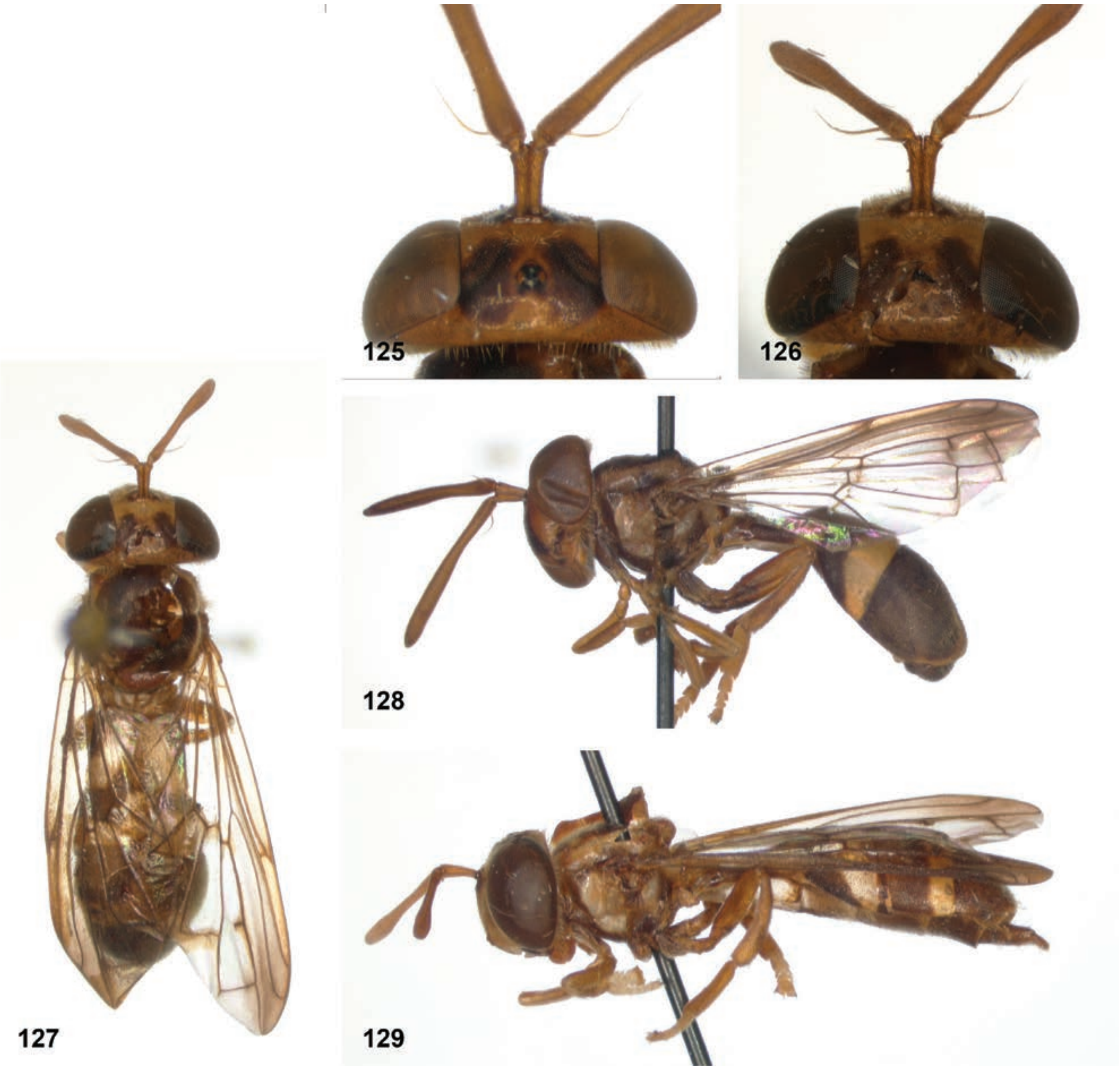


Figures 114–116. *Microdon subpetiolatus* Thompson male, paratype: **114** habitus, dorsal **115** habitus, dorso-lateral **116** head, frontal.

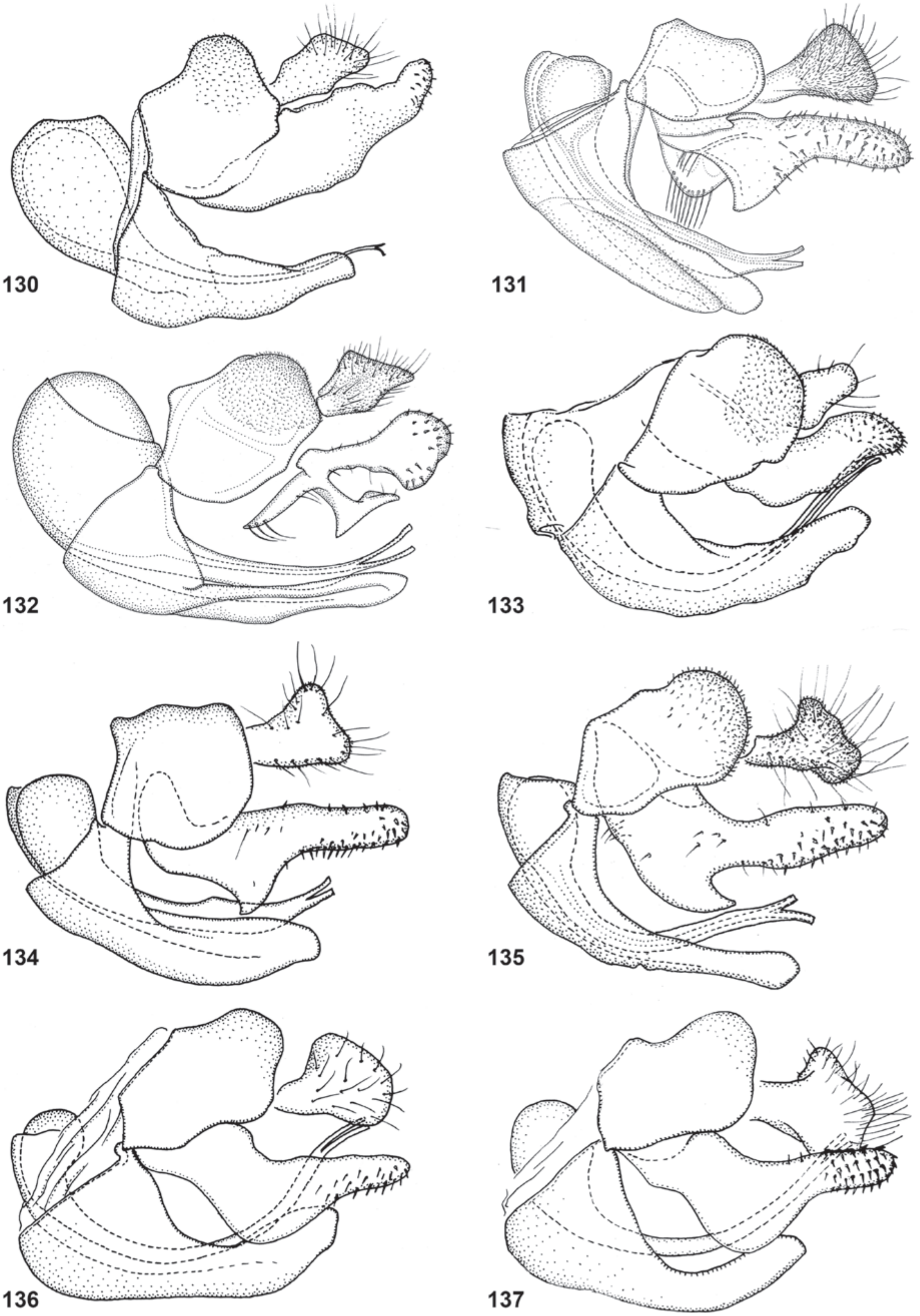


Figures 117–122. *Microdon vespiformis* de Meijere female, lectotype: **117** habitus, dorsal **118** habitus, lateral **119** head, frontal **120** head, lateral **121** head, dorsal **122** wing.

Figures 123, 124. *Paramixogaster wegneri* Keiser male, holotype: **123** habitus, dorsal **124** head, frontal.



Figures 125–129. *Paramixogaster wegneri* Keiser, paratypes: **125** head, dorsal, male **126** head, dorsal, female **127** habitus, dorsal, female **128** habitus, lateral, male **129** habitus, lateral, female.



Figures 130–137. Male genitalia of *Paramixogaster* species: **130** *P. contracta* (paratype *Microdon subpetiolatus* Thompson) **131** *P. halmaherensis* Reemer, sp. nov. holotype **132** *P. luxor* holotype **133** *P. sacki* Taiwan, RMNH **134** *P. sulawesiana* Reemer, sp. nov. holotype **135** *P. jubata* Reemer, sp. nov. paratype Vietnam **136** *P. indica* (paratype *P. wegneri* Keiser syn. nov.) **137** *P. vespiformis* Sumatra, RMNH.

Discussion

For several species of *Paramixogaster* treated in this paper, the taxonomy presented here is not fully satisfying. The main cause for this is the small number of specimens available for most of the species. For nine of the 15 known Oriental species, only the type specimen is known and for another two only one sex is known. For two species (*P. fujianensis* and *P. yunnanensis*) only line drawings of the types could be studied, and for two other ones (*P. brunettii* and *P. huoi* Reemer, nom. nov.) only photographs of the types were studied. This leads to uncertainties in the key and diagnoses. Moreover, the photos in Figs 1–3 demonstrate that there is at least one additional, yet undescribed, Oriental species of *Paramixogaster*. Therefore, we advise caution when using the key and diagnoses, and to always compare specimens carefully with the descriptions and photographs.

Paramixogaster luxor is quite aberrant from the other Oriental species in the presence of scutellar calcars and the short postpedicel (shorter than scape). The surstylus of the male genitalia is also very different from other species in the genus because it is divided into three processes (Fig. 131). Because of these characters, it seems possible that *P. luxor* does not belong in *Paramixogaster*. Analysis of molecular characters could be helpful in recovering the phylogenetic affinities of this species, but so far these are not available.

Acknowledgements

The following persons are thanked for their help with studying material under their care, or for providing information about the collections for which they are responsible: Frederique Bakker and Pasquale Ciliberti (RMNH), Torsten Dikow (USNM), Seraina Klopfstein (NMB), Frank Menzel (DEI), Thomas Pape (ZMUC), Doug Yanega (UCRC), Eliana Buenaventura, Sven Marotzke and Joachim Ziegler (ZMHU). We are grateful to Jeroen van Steenis for providing images of the type of *Mixogaster vespiformis* Brunetti from the collection of the ZSI in Calcutta. We thank Keke Huo for his kind help in enquiring about the types of *Paramixogaster fujianensis* and *P. yunnanensis* at the CASB, and also for sharing with us some photos of the holotype of *Paramixogaster trifasciatus* Huo & Zhao. Thanks also to Doug Yanega for pointing out the (female) gender of the genus name *Paramixogaster*. We also thank Husni Che Ngah for allowing us to use his images of an undescribed *Paramixogaster* from Malaysia. Finally, we thank Greg R. Ballmer for allowing us to use his image of a larva of *Paramixogaster vespiformis* and providing information about this.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

No funding was reported.

Author contributions

All authors have contributed equally.

Author ORCIDs

Hariharakrishnan Sankararaman https://orcid.org/0000-0002-5244-9833

Data availability

All of the data that support the findings of this study are available in the main text.

References

Brunetti E (1913) Zoological results of the Abor expedition. Part II. Chapter XI. Diptera. Records of the Indian Museum 8(1912–1922): 149–190.

Brunetti E (1923) Order Diptera. Families Pipunculidae, Syrphidae, Conopidae, Oestridae. Taylor & Francis, London, 424 pp.

Cheng X-Y, Thompson FC (2008) A generic conspectus of the Microdontinae (Diptera: Syrphidae) with description of two new genera from Africa and China. Zootaxa 1879(1): 21–48. https://doi.org/10.11646/zootaxa.1879.1.3

Cumming JM, Wood DM (2017) 3. Adult morphology and terminology. In: Kirk-Spriggs AH, Sinclair BJ (Eds) Manual of Afrotropical Diptera. Vol. 1. Introductory chapters and keys to Diptera families. Suricata 4: 89–134.

Curran CH (1931) Additional records and descriptions of Syrphidae from the Malay Peninsula. Journal of the federal Malay States Museum 16: 290–338.

de Jong H (2000) The types of Diptera described by J.C.H. de Meijere. Backhuys Publishers, Leiden.

de Meijere JCH (1908) Studien über südostasiatische dipteren. III. Tijdschrift voor Entomologie 51: 189–332.

de Meijere JCH (1917) Studien über südostasiatische dipteren XIII. Tijdschrift voor Entomologie 60: 238–251.

Doleschall CL (1857) Tweede bijdrage tot de kennis der dipterologische fauna van Nederlandsch Indië. Natuurkundig tijdschrift voor Nederlandsch Indië 14: 377–418.

Evenhuis NL, Pape T [Eds] (2022) Systema Dipterorum, version 3.8. http://diptera.org/ [Accessed on 10 July 2022]

Huang C, Cheng X (2012) Diptera Syrphidae. Fauna Sinica. Insecta 50: 1–852.

ICZN (1999) International Code of Zoological Nomenclature. 4th edn. The International Trust for Zoological Nomenclature, London, 306 pp.

Keiser F (1964) *Paramixogaster wegneri*, ein neuer Syrphide von der Insel Ambon, Indonesia (Dipt.). Mitteilungen der Schweizerische Entomologische Gesellschaft 37: 83–87.

Knutson LV, Thompson FC, Vockeroth JR (1975) Family Syrphidae. In: Delfinado D, Hardy DE (Eds) A catalog of the Diptera of the Oriental region 2: 307–374.

Lohman DJ, de Bruyn M, Page T, von Rintelen K, Hall R, Ng PKL, Shih H-T, Carvalho GR, von Rintelen T (2011) Biogeography of the Indo-Australian Archipelago. Annual Review of Ecology, Evolution, and Systematics 42(1): 205–226. https://doi.org/10.1146/annurev-ecolsys-102710-145001

Pendlebury HM (1927) Notes on mimetic insects from the Malay Peninsula. Proceedings of the Entomological Society of London 1: 37–41.

Reemer M (2012) Natural History of Microdontinae (Diptera: Syrphidae): a review. In: Reemer M, Unravelling a hotchpotch, phylogeny and classification of the Microdontinae (Diptera: Syrphidae). PhD thesis, Leiden University. http://hdl.handle.net/1887/18582

Reemer M (2013) Review and phylogenetic evaluation of associations between Microdontinae (Diptera: Syrphidae) and ants (Hymenoptera: Formicidae). Psyche (Cambridge, Massachusetts) 2013(538316): 1–9. https://doi.org/10.1155/2013/538316

Reemer M, Ståhls G (2013a) Generic revision and species classification of the Microdontinae (Diptera, Syrphidae). ZooKeys 288: 1–213. https://doi.org/10.3897/zookeys.288.4095

Reemer M, Ståhls G (2013b) Phylogenetic relationships of Microdontinae (Diptera: Syrphidae) based on molecular and morphological characters. Systematic Entomology 38(4): 661–688. https://doi.org/10.1111/syen.12020

Sack P (1922) H. Sauter's Formosa-Ausbeute: Syrphiden II. (Dipt.). Archiv für Naturgeschichte 87 [1921], A: 1–18.

Shiraki T (1930) Die Syrphiden des Japanischen Kaiserreichs, mit berücksichtigung benachbarter Gebiete. Memoirs of the Faculty of Science and Agriculture. Taihoku Imerial University 1: 1–446.

Ssymank A, Reemer M (2016) A new Afrotropical species of Microdontinae, provisionally placed in *Paramixogaster* (Diptera: Syrphidae). Acta Entomologica Musei Nationalis Pragae 56(1): 403–408.

Tänzler R, Toussaint EFA, Suhardjono YR, Balke M, Riedel A (2014) Multiple transgressions of Wallace's Line explain diversity of flightless *Trigonopterus* weevils on Bali. Proceedings of the Royal Society B 281: 20132528. https://doi.org/10.1098/rspb.2013.2528

Thompson FC (2020) A new *Microdon* ant fly from Sri Lanka (Diptera: Microdontinae). Entomologist's Monthly Magazine 156(2): 87–91. https://doi.org/10.31184/M00138908.1562.4029

Thompson FC, Vockeroth JR (1989) Family Syrphidae. In: Evenhuis NL (Ed.) Catalog of the Diptera of the Australasian and Oceanian Regions. Bishop Museum Press, Honolulu & E.J. Brill, Leiden: 437–458.

Zhao L, Li G, Huo K (2022) Two new species of the tribe Microdontini (Diptera: Syrphidae) from China. Entomotaxonomia 44(4): 1–8. https://doi.org/10.11680/entomotax.2022032

ZooKeys 1208: 49–80 (2024)
DOI: 10.3897/zookeys.1208.122126

Research Article

Taxonomic and nomenclatural reassessment of the Iberian Peninsula's *nomina obscura*, *Scolopendra viridipes* Dufour, 1820 and *S. chlorotes* L. Koch in Rosenhauer, 1856 (Chilopoda, Scolopendromorpha, Scolopendridae)

Carles Doménech[1]

1 *Departament de Ciències Ambientals i Recursos Naturals, Universitat d'Alacant, Carretera de Sant Vicent del Raspeig s/n C.P. 03690, San Vicent del Raspeig, Alacant, Spain*
Corresponding author: Carles Doménech (carles.domenech.perez@gmail.com)

OPEN ACCESS

Academic editor: Alessandro Minelli
Received: 2 March 2024
Accepted: 22 April 2024
Published: 25 July 2024

ZooBank: https://zoobank.org/56CC7AA9-4B0A-4EA0-86A5-B066E6A57FC3

Citation: Doménech C (2024) Taxonomic and nomenclatural reassessment of the Iberian Peninsula's *nomina obscura*, *Scolopendra viridipes* Dufour, 1820 and *S. chlorotes* L. Koch in Rosenhauer, 1856 (Chilopoda, Scolopendromorpha, Scolopendridae). ZooKeys 1208: 49–80. https://doi.org/10.3897/zookeys.1208.122126

Abstract

The taxonomic identities of the two largely neglected *Scolopendra* Linnaeus, 1758 species from continental Spain, *S. viridipes* Dufour, 1820 and *S. chlorotes* L. Koch in Rosenhauer, 1856, are examined in this paper. After efforts in locating both species' type series in eight European institutions, the specimens are considered to be lost. Consequently, the identifications of both taxa were approximated by collating their descriptions with the morphology of all other sympatric Scolopendromorpha. Then, compatible topotypes for both species were collected, and among these a neotype for each taxon were selected and compared with the type series of their respective closest relatives. Finally, both *S. viridipes* and *S. chlorotes* are proposed to be conspecific with *S. oraniensis* Lucas, 1846. Therefore, the name *S. viridipes* is here established as (senior) **syn. nov.** and **nomen oblitum** of *S. oraniensis*, *S. oraniensis* is declared as **nomen protectum,** and *S. chlorotes* (junior) **syn. nov.** is reallocated to *S. oraniensis*. Moreover, the specimens making up the type series of *S. oraniensis* are also indicated and redescribed, the genitalia are illustrated for the first time, and its specific epithet is briefly reviewed, remaining unaltered in respect of its original spelling.

Key words: Chilopoda, *chlorotes*, continental Spain, *oraniensis*, *Scolopendra*, *viridipes*

Introduction

The class Chilopoda Latreille, 1817 is a group of venomous terrestrial predators that play an important ecological role in the warm and temperate ecosystems. Taxonomically, this group of arthropods encompasses approximately 3,100 species distributed in five orders (Minelli 2011). The best known of all of them is the order Scolopendromorpha, which currently counts a total of six accepted families subdivided into 37 genera and subgenera (Schileyko et al. 2020).

In peninsular Spain, the order Scolopendromorpha is represented by three of those six families. One of them, Plutoniumidae Bollman, 1893 (Fig. 1A), is composed of two extant genera: the monotypic *Plutonium* Cavanna, 1881 and

Theatops Newport, 1844, the latter only represented by a single species. The second family, and the most diverse one in the peninsula, is the monotypic family Cryptopidae Kohlrausch, 1881 (Fig. 1B). This taxon includes two *Cryptops* Leach, 1814 subgenera, and a total of eight species. The third is the family Scolopendridae Leach, 1814 (Fig. 1C–I), which is represented by one genus, *Scolopendra* Linnaeus, 1758, and two reported taxa, *S. cingulata* Latreille, 1829 and *S. oraniensis* Lucas, 1846 (Vadell 2013; Giribet 2015; Bonato et al. 2017b).

With the general exception of the north and northwest, these two *Scolopendra* species are widely and almost sympatrically distributed in continental Spain (Serra 1983; García-Ruiz 2018; Cabanillas 2019; Cabanillas et al. 2019; Cabanillas and Parejo-Pulido 2019; Cabanillas and García-Febrero 2020; Doménech et al. 2023). *Scolopendra cingulata* is the longest, reaching up to 80–90 mm (García-Ruiz 2007). Even as a juvenile, this species has a characteristic colouration of yellow tergites posteriorly pigmented by a blackish horizontal band—the "*cingulum*"; from Latin for belt or cord—that distinguishes it by sight from its local Iberian relatives (Fig. 1C). The other species, *S. oraniensis*, still often incorrectly referred to as a *S. canidens* Newport, 1844 subspecies (Würmli 1980; Serra 1983; Carballo and Daza 1991; García-Ruiz 1993, 2018), is a smaller centipede which only reaches up to 65 mm. Its colouration is the most variable within the Iberian Scolopendromorpha, with legs and antennae from pale yellow to greenish, blueish, or reddish, and the dorsal habitus with various combinations of colour from cream to dark brown that can vary even sympatrically (Fig. 1D–I).

However, besides *S. semipedalis* Dufour, 1820 (= *Himantarium gabrielis* (Linnaeus, 1767), see Bonato and Minelli 2014) and *S. venefica* L. Koch in Rosenhauer, 1856 (= *S. cingulata*, see Attems 1930), two additional and until now largely forgotten species from the Iberian Peninsula were included in the genus *Scolopendra*. The first one is *S. viridipes* Dufour, 1820, a lapidicolous and small-sized centipede described from an unspecified place in the "Mountains of Kingdom of Valencia" (east of continental Spain) (Fig. 2A–C). Aside from the description and subsequent transcription (Lucas 1840), the literature on this species is mostly limited to species lists (Gervais 1837; Lamarck 1838, 1839; Lucas 1840; Laboulbène 1865). However, based only on the literature, some authors hypothesised about its taxonomic relationships and actual identity: Brandt (1840) and Ranzani (1841) considered that *S. clavipes* C. L. Koch, 1836 [not 1847, see Doménech and Nagel 2022] could actually be a junior synonym of this species. Walckenaer and Gervais (1844) concluded that *S. viridipes* was too poorly described for proper recognition, while Pirotta (1878a) questioned whether his own recently described species, *S. doriae* Pirotta, 1878b (= *S. cingulata*), was simply another synonym of *S. viridipes*. Soon after, Kraepelin (1903) listed *S. viridipes* [as ?*S. viridipes* Dufour, 1860 (sic.)] as a possible synonym of *S. oraniensis*, and finally, Attems (1930) included *S. viridipes* Dufour, 1822 (sic.) in the list of "non-recognizable taxa".

The second species in this underappreciated group is *S. chlorotes* L. Koch in Rosenhauer, 1856, another small, but much better described taxon from "near Málaga", Andalusia (south of continental Spain) (Fig. 2A, D, E). Only four references to this species were found that include its original description, a transcription (Rosenhauer 1856) and two taxonomic mentions: *S. chlorotes* was also listed by Kraepelin (1903) as a possible synonym of *S. oraniensis*, while Attems (1930) declared *S. chlorotes* as an unrecognisable species.

After more than nine decades of bibliographic silence, the uncertain taxonomic and nomenclatural identities of the two enigmatic species *S. viridipes* and *S. chlorotes* are now evaluated, a specific diagnosis for each species is given, and the nomenclatural situation for these taxa is finally clarified.

Figure 1. Representatives of Scolopendromorpha from the Iberian Peninsula (uncollected) **A** family Plutoniumidae Bollman, 1893: *Theatops erytrocephalus* (C. L. Koch, 1847), Seoane do Caurel, Lugo (credit: J. Tizón) **B** family Cryptopidae Kohlrausch, 1881: *Cryptops* sp. Leach, 1814, Villena, Alacant (credit: D. Molina) **C–I** family Scolopendridae Leach, 1814 **C** *Scolopendra cingulata* Latreille, 1829, Benilloba, Alacant (credit: M. Huesca and CD) and **D–I** *S. oraniensis* Lucas, 1840. Observe that in this species the colour variants can occur sympatrically **D, H, I** Benilloba, Alacant and **E–G** Almeria Province, Andalucia (credit: F. Rodriguez Luque).

Materials and methods

The depositories of the types series of *Scolopendra viridipes*, *S. chlorotes*, and *S. oraniensis* were scrutinised following the texts of Dufour (1820), Lucas (1846), L. Koch (1856), Kraepelin (1904), Rühm (1925), Moritz and Fischer (1979) and Hessel (2000). The additional data from the depositories were obtained from https://www.idigbio.org, https://bionomia.net, and http://sdei.senckenberg.de/biographies websites (last accessed on 21 Jan. 2022). Depository and other institutions abbreviations are as follows:

ASU	Altai State University, Altai Krai, Russia
CEUA	Colección Entomológica de la Universidad de Alicante San Vicent del Raspeig, Alacant, Spain
CLD	Cercle Léon Dufour. Saint Severe, Nouvelle-Aquitaine, France
FAU	Friedrich-Alexander Universität, Erlangen-Nürnberg, Erlangen, Germany
MNCN	Museo Nacional de Ciencias Naturales, Madrid, Spain
MNHN	Muséum national d’Histoire Naturelle, Paris, France
MZS	Musée Zoologique, Strasbourg, France
NHMB	Naturhistorisches Museum Bern, Bern, Switzerland
NHMN	Naturhistorisches Museum Nürnberg, Nürnberg, Germany
NHMUK	Natural History Museum, London, UK
SAE	Sociedad Andaluza de Entomología, Dos Hermanas, Sevilla, Spain
SLB	Société Linnéenne de Bordeaux, Bourdeaux, France
UPV	Universitat Politècnica de València, València, Spain
ZMB	Museum für Naturkunde, Berlin, Germany

Topotypes locations of *Scolopendra viridipes* are based on information given in Dufour (1888), Hessel (2000), and Ferrández (2020). From these, only the inland mountainous localities with Dufour’s (1820) description of colour-matching specimens were chosen (Fig. 2A–C). *Scolopendra chlorotes* topotypes were collected in the surrounding areas of Málaga City and in the municipality’s surroundings following L. Koch (1856) (Fig. 2A, D, E). Specimens from these areas, representing the nominal species *S. viridipes* and *S. chlorotes*, were manually collected and soaked in 50% ethanol for 15 min. For preservation of the samples, individual containers with 70% ethanol were used. Morphological features were checked and photographed under a Leica M205C stereomicroscope connected to a montage imaging system, Leica DFC450, operated under the Cell’D program at the Universidad de Alicante (**UA**), Spain. Measurements were made with a Monzana® Digital Vernier Caliper. All specimens were collected following the indications in permits granted by the Generalitat Valenciana (Exp. 093/20 FAU20_006; grant date: 17 Feb. 2020) and Junta de Andalucía (N/Ref.: SGYB/DBP; grant date: 15 May 2021). Throughout the text, the term topotype [without quotation marks] will refer to specimens collected at the type locality of the original descriptions. The term “topotype”, with quotes, indicates that they have lost this original topotype designation in favour of the one of the neotype (ICZN 1999: Art. 76.1.1, 76.1.6).

The type series of *Scolopendra oraniensis* in the MNHN was identified following Lucas (1840) and Kraepelin (1904), as well as the label information found in the jars. All specimens were examined using a Wild Heerbrugg M3C stereomicroscope at the MNHN. Illustrations of morphological features were achieved using a Canon digital camera model EOS 6D with a MP-E 65 mm lens operated with Helicon Remote v. 3.9.1.W system. Morphological abbreviations used in text are as follows:

General morphology

AP	apical spines
DM	dorso-median spines
LS	lateral spines
M	median spines
S, **SS**	sternite, sternites
SAP	subapical spines
SP	prefemoral process spines
T, **TT**	tergite, tergites
UL	ultimate legs
ULBS	ultimate leg-bearing segment
V	ventral spines
VL	ventro-lateral spines
VM	ventro-median spines

Genital region

AV	anal valve
LA	lamina adanalis
LS	lamina subanalis
SGS I	sternite of genital segment 1
SGS II	sternite of genital segment 2

The species identifications and differential diagnosis in Tables 1, 2 are based on the previous works of Dufour (1820), Lucas (1846), L. Koch (1856), Cavanna (1881), Kraepelin (1903), Ribaut (1915), Attems (1930), Verhoeff (1931, 1934), Machado (1953), Matic and Darabantu (1968), Würmli (1980), Serra (1981, 1983), Iorio and Geoffroy (2006, 2008), Di et al. (2010), Lewis (2010, 2011), Vadell (2013), Voigtländer and Reip (2013), Giribet (2015), Bonato et al. (2017b), and Schileyko et al. (2020).

The distribution of *Scolopendra* species colour variants were defined using the **BV** (Biodiversidad Virtual 2024) website with only the confirmed identifications of D. Cabanillas (BV's expert) and the author together with the texts of Voigtländer and Reip (2013), Cabanillas and García-Febrero (2020), and field observations. Standardised nomenclature for centipede morphology was applied following Bonato et al. (2010). Sex determination and genitalia descriptions have been performed using Demange and Richard (1969), Iorio (2003), Iorio and Geoffroy (2006), and Siriwut et al. (2016). Nomenclatural acts, including the neotypes designations, were made according to the rules of the Arts. 23.2, 23.3, 23.9.1.1, 23.9.1.2, 23.9.2, 23.9.6, 32.5, 58, 58.15, 72.4.1.1, 73.1.2, 74.7, 75.1–75.3, and 76 in the fourth edition of the International Code of Zoological Nomenclature (ICZN 1999).

Background removal in illustrations, contrast adjustments, map configuration, and their respective clarifying notes were performed with Adobe Photoshop CS6 software®. A base map was obtained from the National Oceanic and Atmospheric Administration, National Weather Service (NOAA/NWS 2022) website.

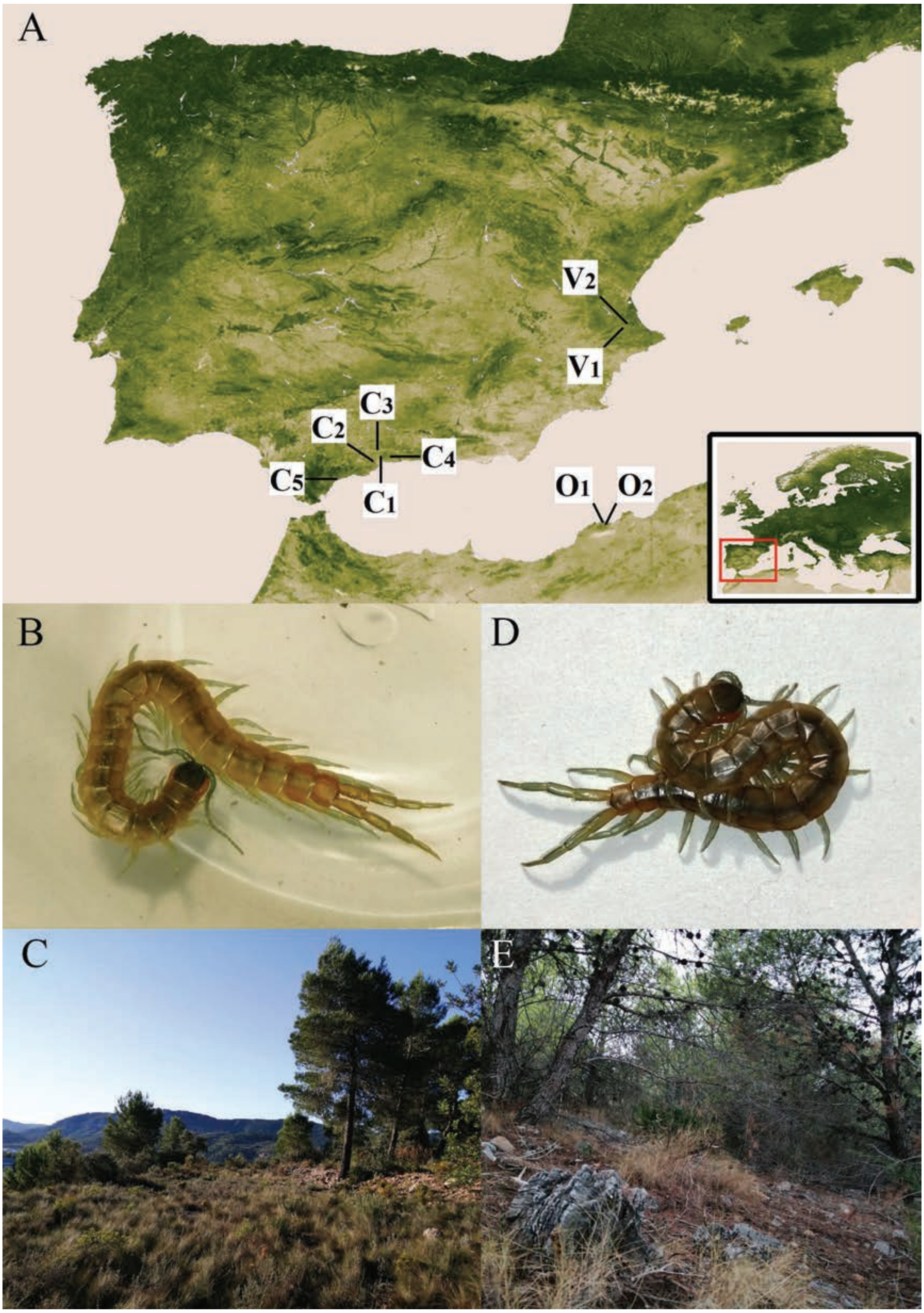


Figure 2. A topotype collection localities in the Iberian Peninsula (southwestern Europe): *S. viridipes* topotypes (= *S. oraniensis*); V_1 = Moixent and V_2 = Xàtiva (previously San Felipe), Valencia province, Valencian Country/Community, Spain and *S. chlorotes* topotypes (= *S. oraniensis*); C_1 = Málaga municipality, C_2 = Alahurín de la Torre, C_3 = Casabermeja, C_4= Totalán and C_5 = Estepona, Málaga province, Andalucía, Spain. The "O" points *S. oraniensis* type localities, O_1 = Santon's mountains [corrected from "Sauton" (sic.); Lucas 1846] and O_2 = "Between Oran and Mers-el-Kebir", Oran province (Wilayah), Algeria **B** "*S. viridipes*" topotype 2, female, (CEUAMr22) from **C** Moixent, Alacant **D** "*S. chlorotes*" topotype 6, female, (CEUAMr30) from **E** Alahurín de la Torre, Málaga.

Material examined

CEUA: **Spain** • 2♂ and 2♀ adults *S. viridipes* “topotypes” (CEUAMr21–25): Valencia Province: Moixent; Embassament del Bosquet, (38°51'21.7"N, 0°44'36.7"W 380 m a.s.l.) (Fig. 2B, C), 1 ♂ (Neotype, CEUAMr005, Figs 3, 4, Table 3, Suppl. material 1: file 1) and 1♀; Coll. 26 Sep. 2020 and 1 ♂ and 1♀ Xàtiva, Pujada Bixquert (38°58'56.4"N, 0°30'25.7"W, 115 m a.s.l.); Coll. 3 Oct. 2020, Lapidicolous; C. Doménech leg. (Figs 2A–C, 3, 4, 9A, C; Table 3; Suppl. material 1: file 1). • 4 ♂, 8♀ (1 subadult) and 3 unsexed (1 subadult) individuals *S. chlorotes* “topotypes” (CEUAMr25 to 39): Málaga province, 4♀ (1 subadult), Málaga Municipality, next to park Cementerio (36°43'27.7”N, 4°31'10.8”W 71 m a.s.l.); 1 ♂ (Neotype, CEUAMr29, Figs 5, 6; Table 3; Suppl. material 1: file 3) and 1♀, Alahurín de la Torre, Carretera de Coín, (36°39'37”N, 4°31'0.4”W 104 m a.s.l.) (Fig. 2D, E); 1 ♂, 2♀ and 1 unsexed adults; Casabermeja, el Chorro, (36°59'14.9”N, 4°25'52.5”W 649 m a.s.l.); 2 ♂ and 1 unsexed subadult, Totalán, Arroyo de Sixto (36°45'04.1”N, 4°18'41”W 154 m a.s.l.); Coll. 18 and 19 Nov. 2021; C. Doménech Leg.; 1♀ and 1 unsexed, Estepona (36°25'59"N, 5°07'59"W 115m a.s.l.), Coll. 17 Jun. 2021. R. Perez Ríos leg. Lapidicolous (Figs 2A, D, E, 5, 6, 9B, D; Table 3; Suppl. material 1: file 3).

MNHN: **Algeria** • 7 unsexed adults (2 probable females) *S. oraniensis* (type series); Oran’s wilayah; Santon’s mountains (corrected from “Sauton” (sic.) Lucas 1846 (ca 35°44'03"N, 7°08'16"W) and between Oran and Mers-el-Kebir (ca 35°43'40"N, 0°42'29"W); P.H. Lucas Leg. In ravines, lapidicolous (Figs 7, 8; Table 3).

Systematics

Order Scolopendromorpha Pocock, 1895
Family Scolopendridae Leach, 1814
Subfamily Scolopendrinae Kraepelin, 1903
Tribe Scolopendrini Leach, 1814
Genus *Scolopendra* Linnaeus, 1758

Scolopendra viridipes Dufour, 1820

Figs 2B, 3, 4, 9A, C, Table 3, Suppl. material 1: file 1

Scolopendra viridipes Dufour, 1820: 317.
?*S. clavipes* C. L. Koch, 1836 [1847 sic.]: Brandt (1840): 149; Ranzani (1841): 441.
S. viridipes: Walckenaer and Gervais 1841: 258, as unrecognisable taxon.
?*S. doriae* Pirotta, 1878a (= *S. cingulata*): Pirotta 1878b: 406.
?*S. oraniensis* Lucas 1846: Kraepelin 1903: 246, as “?*S. viridipes* Dufour, 1860" (sic.).
S. viridipes [Dufour, 1822 sic.]: Attems 1930: 51, as unrecognisable taxon.

Etymology. From Latin *viridis* (green) and *pes* (feet), literally meaning green-footed *Scolopendra*.

Type series and type depository. Types currently lost.

Collector and collection date. J. M. L. Dufour, between 1811 and 1813 (Dufour 1888; Hessel 2000; Ferrández 2020).

Type locality. “Kingdom of Valencia”, Valencian Community, east of Spain.

Distribution. As for type locality.

Neotype designation. With the express purpose of clarifying the taxonomic status and the type locality of the nominal taxon *S. viridipes* Dufour, 1820, the following neotype for this species is designated (ICZN 1999: Art. 75 and 76.3):

Male. Embassament del Bosquet, Moixent; Valencia Province (Spain) (38°51'21.7"N, 0°44'36.7"W 380 m a.s.l.) (Figs 3, 4; Table 3; Suppl. material 1: file 1). Coll. 26 Sep. 2020. C. Doménech leg. Repository in CEUA with the collection number CEUAMr21 (In this text also referred to as *S. viridipes* "topotype 1" before its neotype designation).

Proposed new nomenclatural status. *S. viridipes* Dufour, 1820 is an invalid name subjectively designated here as nomen oblitum and a senior synonym of *S. oraniensis* Lucas, 1846.

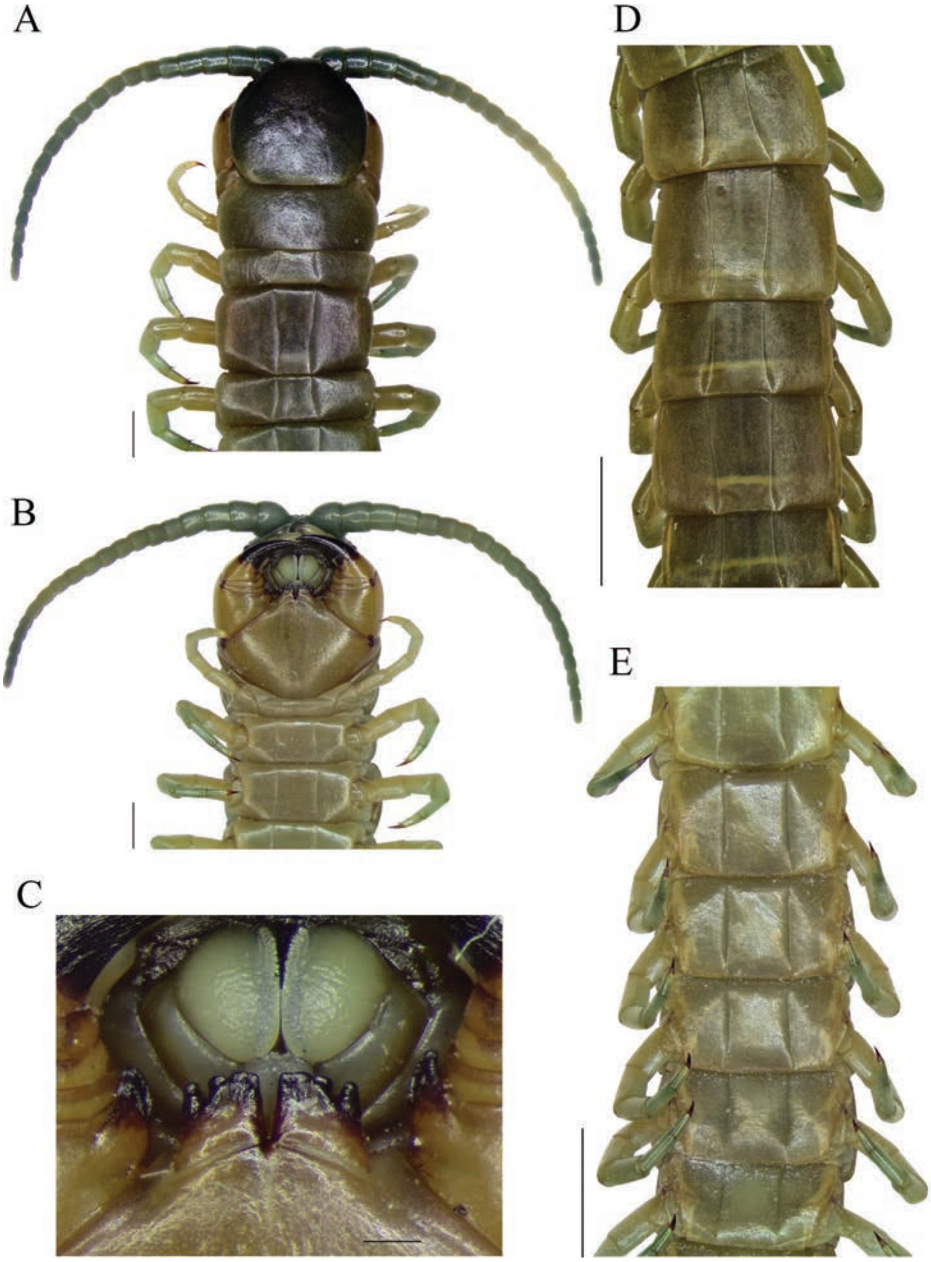


Figure 3. *Scolopendra viridipes* neotype (= *S. oraniensis*); male; ("topotype 1", CEUAMr21) **A** cephalic plate, antennae, and TT 1–5 **B** forcipular segment and sternites 1–3 **C** tooth plates **D** tergites 13–18 **E** sternites 10–15. Scale bars: 0.2 mm (**C**); 1 mm (**A, B**); 2 mm (**D, E**).

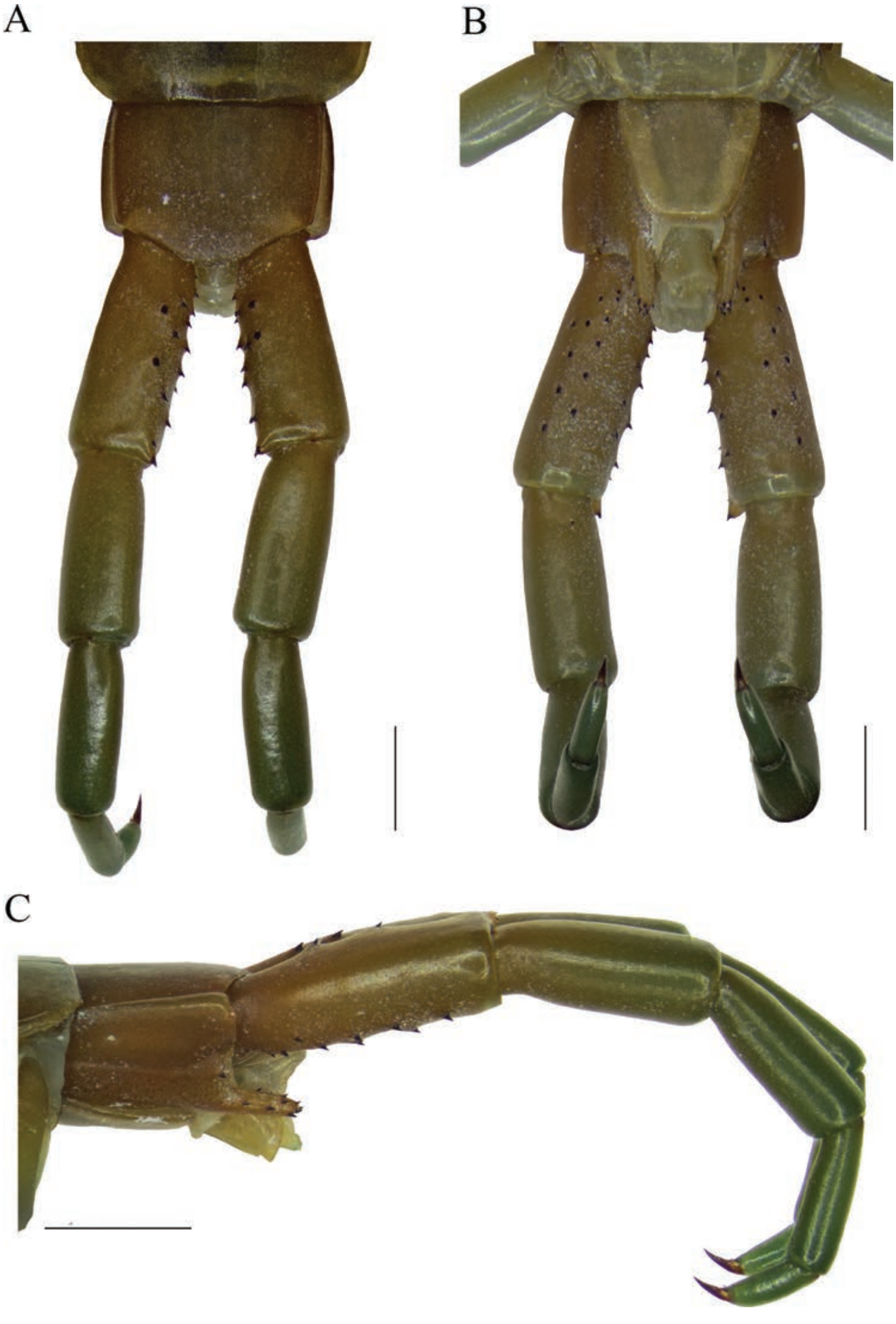


Figure 4. *Scolopendra viridipes* neotype (= *S. oraniensis*); male; ("topotype 1", CEUAMr21) **A** ULBS and UL's dorsal view **B** ULBS's and UL's ventral view **C** ULBS's, coxopleuron, and UL's ventral lateral view. Scale bars: 1 mm (**A, B**); 2 mm (**C**).

Translation of the original descriptions from Latin and French. [annotations in brackets]. (Original description available from: https://books.google.be/books?vid=GENT900000003803&printsec=frontcover#v=onepage&q&f=false)

XII. Green-footed Scolopendra

Scolopendra (viridipes) shell [dorsal habitus; tergites] livid, antennae and feet [legs] greenish, 21 feet [legs] in each side, the posterior ones longer.

Habitat: under the rocks of the Valencian Kingdom's mountains. Length 18 lignes [1 Paris ligne = 2.2556 mm; 40.6 mm].

It differs from *Scol. morsitans*. The body segments [sensu tergites] are roughly square and equal between them, except for the first two and the last one. The head [cephalic plate] is small and oval. The whole body [dorsal habitus] has a markedly livid colour. The legs and the antennae are greenish. They [antennae] end in a setaceous point and have more than fifteen articles. The legs grow from the head [cephalic plate] to the anus [ultimate leg-bearing segment; ULBS]. The palps [first maxillary telopodites] end with a dilated and round article [article 3].

Remarks involving the type series and type series depository. Efforts to locate *S. viridipes* type series in its four most probable repositories, CLD, MNHN, MNCN, and SLB, were unsuccessful (J. J. Geoffroy (MNHN) and B. Sánchez (MNCN) pers. comm. May 2020 to Oct 2021; CD pers. obs.).

Knowing that Dufour mostly preserved his specimens in dry conditions (Dufour 1888; Ferrández 2020), it is conceivable that the major part of his material was degraded by subsequent insufficient curatorial handling (Ferrández 2020; MA Ferrández pers. comm. May 2020–Oct. 2021).

Therefore, the *S. viridipes* type series is here considered as definitively lost material.

Original description comparison. Because the type material for *S. viridipes* has vanished, and to determine to which species Dufour (1820) was referring, the available characters for this taxon are compared with all other Scolopendromorpha from Peninsular Spain (Table 1).

Initially, the brief morphological description does not allow one to assign *S. viridipes* to any definite genus because some features are common for all Scolopendromorpha, either because they are insufficiently detailed or widely observed (See "*" in Table 1). *Cryptops* (*C.*) *lobatus* Verhoeff, 1931, *C.* (*T.*) *longicornis* (Ribaut, 1915), as well as *Plutonium zwierleini* Cavanna, 1881 should be discarded as candidates for the application of the name *S. viridipes*, due to the fact that their restricted distributional areas are outside of those of this species.

The six remaining *Cryptops* species (Fig. 1B) are smaller than *S. viridipes*, except for *C.* (*C.*) *anomalans* Newport, 1844. This rules out five of those taxa as candidates for this name (Table 1). *Theatops erythrocephalus* (C. L. Koch, 1847) can be similar in size to *S. viridipes*; however, it can be assumed that Dufour was actually not referring to *T. erythrocephalus* when he described *S. viridipes*, since he did not highlighted the conspicuous ultimate leg (UL) width, but pointed out a longer length; nor did he highlight the enlarged size of segment 21, remarking instead on the different sizes and shapes of TT1, 2, and 21, being these presumably smaller than the TT3–20 (Table 1). These are all distinctive traits for *T. erythrocephalus* (Fig. 1A).

Otherwise the exclusive colouration of *S. viridipes*, a "livid" dorsal habitus with greenish legs and antennae (Figs 2B, 3, 4), is an exclusive feature that clearly distinguishes it from all other Iberian Scolopendromorpha, with one exception, *S. oraniensis*. This colouration eliminates *T. erythrocephalus* and all the Iberian cryptopids as candidates because they all have consistently pale yellowish to reddish integuments and appendages, with no greenish pigmentation (Fig. 1A, B).

Scolopendra cingulata always has tergites with posterior transverse black pigmentation combined with shiny red, orange, or yellow colouration in their legs when juvenile (Voigtländer and Reip 2013), or pale yellow legs when in an adult stage (Fig. 1C). Rarely, some adult individuals of *S. cingulata* from central and western Spain can exhibit a barely discernible green shade on the anterior and/or posterior locomotory legs and basal antennae articles (i.e., Cabanillas and García-Febrero 2020). This pigmentation is absent in the populations surrounding València, the type locality of *S. viridipes* (Fig. 2A; BV 2024).

The remaining Scolopendromorpha species inhabiting the presumed type locality of *S. viridipes* is *S. oraniensis*. This species is variable in colouration even within local populations (Fig. 2D–I; BV 2024); however, the pale and greenish habitus is by far one of the most frequent variations in Valencia. Therefore, because of its compatible distribution, size, morphology, and colouration, *S. oraniensis* is a good candidate to be the species to which Dufour was actually referring under the name *S. viridipes* (Table 1, Suppl. material 1: file 1).

Hence, prior to analysing some compatible topotypic material, all features stated in the original description strongly suggest that the closest relative to *S. viridipes* is *S. oraniensis*, if they do not belong to the same taxon.

Neotype and “topotypes” morphological comparisons. Four colour-, morphological-, and size-compatible *S. viridipes* topotypes were collected in two Valencian localities known by their authorities (Figs 2B, 3, 4). All these specimens were examined and confirmed to be conspecific (Suppl. material 1: file 1). From those a neotype was selected (ICZN 1999: Art. 75; Figs 3, 4; Table 3; Suppl. material 1: file 1). The comparison of the neotype and other “topotypes” with the syntypes of the closest relative, *S. oraniensis* (Table 1) confirmed that all of them shared identical diagnostic features (Table 3; compare Figs 3, 4 with Figs 7, 8). Hence, according to all the data presented above, *S. viridipes* and *S. oraniensis* are here designated to be conspecific taxa.

Taxonomic and nomenclatural status. As the two taxa, *S. viridipes* Dufour, 1820 and *S. oraniensis* Lucas, 1846, are deemed to be conspecific, the “Principle of Priority” provides preference for the name *S. viridipes* to replace the name *S. oraniensis* (ICZN 1999: Art. 23, 23.2, 23.3). However, we propose the nomenclatural reversal of precedence (ICZN 1999: Art. 23) in favour of the prevailing usage and nomenclatural stability of the largely accepted name *S. oraniensis* since the two conditions in Art. 23.9 (ICZN 1999) are met:

1) “the senior synonym [*S. viridipes*] […] has not been used as a valid name after 1899" (ICZN 1999: Art. 23.9.1.1).
   This statement is not strictly true, since Kraepelin (1903) and Attems (1930) did use that name after 1899. Nevertheless, the use of the name in those two publications satisfy the Art. 23.9.6 (ICZN 1999), which clarifies that “the mentioning of a name in a synonymy [Kraepelin 1903], or [...] list of names [Attems 1930] must not be taken into account in determining usage under Art. 23.9.1.1 and 23.9.1.2".
2) “[*S. oraniensis*] has been used [...] as its presumed valid name, in at least 25 works, published by at least ten authors in the immediately preceding 50 years and encompassing a span of not less than ten years” (ICZN 1999: Art. 23.9.1.2; see Suppl. material 1: file 2).

Hence, the name *S. viridipes* is here declared invalid since this is subjectively considered a senior synonym and nomen oblitum of *S. oraniensis*, while the name *S. oraniensis* is proposed as a nomen protectum, being fixed for unequivocal referencing of this species (ICZN 1999: Art. 23.9.2).

Table 1. The original descriptive morphology of *Scolopendra viridipes* in comparison to other Scolopendromorpha species described in Peninsular Spain. **Bold letters** indicate compatible features in other species. * indicates common to the entire Scolopendromorpha, interpretable, or poorly differentiated feature. Nr^{pp}= Not reported, presence possible.

	***Scolopendra viridipes* Dufour, 1820**	***S. cingulata* Latreille, 1829**	***S. oraniensis* Lucas, 1846**	***Cryptops (Cryptops) anomalans* Newport, 1844**	***C. (C.) hispanus* Brölemann, 1920**	***C. (C.) hortensis s.s* (Donovan, 1810)**	***C. (C.) lobatus* Verhoeff, 1931**	***C. (C.) parisi s.s* Brölemann, 1920**	***C. (C.) trisulcatus* Brölemann, 1902**	***C. (Trygonocryptops) longicornis* (Ribaut, 1915)**	***C. (T.) similis* Machado, 1953**	***Plutonium zwierleini* Cavanna, 1881**	***Theatops erythrocephalus* (C. L. Koch, 1847)**
Presence in Valencianish Kingdom	Present	**Present**	**Present**	Nr^{pp}	**Present**	Nr^{pp}	Absent	Nr^{pp}	Nr^{pp}	Absent	Nr^{pp}	Absent	**Present**
Ecology	Edaphic epigean (Lapidicola)	**Edaphic epigean**, troglophile	**Edaphic epigean,** troglophile	**Edaphic epigean**	**Edaphic epigean,** troglophile*	**Edaphic epigean,** troglophile*	**Edaphic epigean**	**Edaphic epigean**	**Edaphic epigean**	Troglobiotic	**Edaphic epigean**	**Edaphic, hipogean,** troglophile	**Edaphic epigean,** troglophile
Colouration	Marked pale, with antenna and legs greenish	Tergites yellowish ended with black distal edge, legs and antenna yellow to orange	**Pale cream to dark green or brown with antenna and legs yellowish, greenish, bluish or reddish**	Pale yellow to reddish	Pale yellow to reddish	Reddish, sometimes pale yellow	Pale yellow to reddish	Reddish	Pale yellow	Pale yellow	Pale yellow	Pale reddish, legs and antennae usually yellowish	Pale yellow to reddish, cephalic plate and UL usually darker
Length (in mm)	40.6 (18 lignes)	100-155	**40-65**	**20-40**	16-30	12-30	10-13.5	14-21	15-35	**27-38**	30	**50-80**	**20-45**
Antennal articles' number*	More than 15*	**18**	**18-19**	**17**	**17**	**17**	**17**	**17**	**17**	**17**	**17**	**17**	**17**
Antennae end in a setaceous point*	Yes*	**Yes**	**Yes**	**Yes**	**Yes**	**Yes**	**Yes**	**Yes**	**Yes**	**Yes**	**Yes**	**Yes**	**Yes**
Headplate shape*	Small* and oval	**Oval**	**Oval**	**Oval**	**Oval**	**Oval**	**Oval**	**Oval**	**Oval**	**Oval**	**Oval**	**Oval**	**Oval**
Shape of the distal palp's article (article 3 in second maxillae's telopodite) *	Dilated and round *	**Subcylindrical**	**Subcylindrical**	**Subcylindrical**	**Subcylindrical**	**Subcylindrical**	**Subcylindrical**	**Subcylindrical**	**Subcylindrical**	**Subcylindrical**	**Subcylindrical**	**Subcylindrical**	**Subcylindrical**
1st, 2nd and last tergites different in shape respect the others*	Yes*	**Yes,** smaller in comparison	**Yes,** smaller in comparison	**Yes,** smaller in comparison	**Yes,** smaller in comparison	**Yes,** smaller in comparison	**Yes,** smaller in comparison	**Yes,** smaller in comparison	**Yes,** smaller in comparison	**Yes,** smaller in comparison	**Yes,** smaller in comparison	**Yes,** 1st and 2nd smaller in comparison, the 21st much bigger	**Yes,** 1st and 2nd smaller in comparison, the 21st much bigger
Ultimate legs length respect the locomotory legs	Longer than locomotor ones	**Longer than locomotor ones**	**Longer than locomotor ones**	**Longer than locomotor ones**	**Longer than locomotor ones**	**Longer than locomotor ones**	**Longer than locomotor ones**	**Longer than locomotor ones**	**Longer than locomotor ones**	**Much longer than locomotor ones**	**Longer than locomotor ones**	Similar in length to locomotor ones, shape markedly thicker	Similar in length to locomotor ones, shape markedly thicker

***Scolopendra chlorotes* L. Koch in Rosenhauer, 1856**

Figs 2D, E, 5, 6, 9B, D, Table 3, Suppl. material 1: file 3

Scolopendra chlorotes L. Koch in Rosenhauer, 1856: 417.
?*S. oraniensis* Lucas, 1846: Kraepelin 1903: 246.
S. chlorotes: Attems 1930: 49, as unrecognisable taxon.

Etymology. From the Greek word *χλοερός* (*khloerós*, verdant) and *χλόη* (*khlóē*, "the green of new growth") meaning greenish yellow, pale green, pale, pallid, or verdant, referencing their pale greenish and yellowish leg colouration.

Type series and type depository. Types currently lost.

Collector and collection date. W. G. Rosenhauer, in 1849 (Rosenhauer 1856).

Type locality. "Near Málaga", Andalusia, Spain.

Distribution. As for type locality.

Neotype designation. With the express purpose of clarifying the taxonomic status and the type locality of the nominal taxon *S. chlorotes* L. Koch in Rosenhauer, 1856, the following neotype is designated (ICZN 1999: Art. 75 and 76.3):

Male. Carretera de Coín, Alahurín de la Torre, Málaga province (Spain) (36°39'37"N, 4°31'0.4"W 104 m a.s.l.) (Figs 5, 6; Table 3; Suppl. material 1: file 1). Coll. 18 Nov. 2021. C. Doménech Leg. Repository CEUA with the collection number CEUAMr29 (In this text also referred as "*S. chlorotes* topotype 5" before its neotype designation).

Proposed new nomenclatural status. *Scolopendra chlorotes* L. Koch in Rosenhauer, 1856 is an invalid name, here subjectively proposed as a junior synonym of *Scolopendra oraniensis* Lucas, 1846.

Translation of the original descriptions from German [annotations in brackets]. (Original description available from: https://www.biodiversitylibrary.org/page/42185817#page/425/mode/1up)

Scolopendra chlorotes Koch.

Brownish green, feeding pliers [forcipules], end-shield [ULBS tergite] and last pair of legs [terminal legs] reddish brown, on the last seven tergites, a furrow at the lateral edges [margination in tergites], on the first podomere of the last pair of legs [UL prefemur] 19 small teeth on the underside [ventral position], seven small teeth directed inward on the upper-side [medial and dorsomedial positions].

Length 20 'lignes' [1 German – Nuremberg – lignes ≈ 2.11 mm; 42.22 mm].

Shiny; head [cephalic plate] longish, rather narrow, the head area dentate [probably referring to tooth plates] in the middle, tergite sides straight, those of the 3rd and the penultimate tergite rounded anteriorly, the seven last tergites with a furrow at the lateral edges [tergite margination]. Tergites with the two normal stripes [paramedian sutures], except the first and the last tergites; the end-shield [ULBS tergite] shows a distinct median longitudinal furrow [suture]. The sternites have two longitudinal furrows [paramedian sutures], except the last sternite. The last pair of legs short, dorsally flat, the tooth-like process at the inner angle of the first podomere short [UL prefemoral process] with two blunt teeth [spines] at the tip; at the inner side [medial position] of this podomere [UL prefemur] seven small teeth [spines] at the upper side [medial position], 19 small teeth [spines] arranged in four rows at the underside [ventral position]. Head [cephalic plate], antennae, and tergites, except the last one, brownish green, the first podomeres [prefemur, femur, and even tibia] of the legs yellowish, the last [tibia and tarsi 1 and 2] green; maxillipeds, lower lip [probably trochanterprefemoral parts of the forcipula, tooth plates or/and coxosternite], end-shield [ULBS tergite] and last pair of legs [UL] reddish brown, the capture-claw [forcipules] brownish black from the middle [tarsungula].

Near Malaga, sporadic.

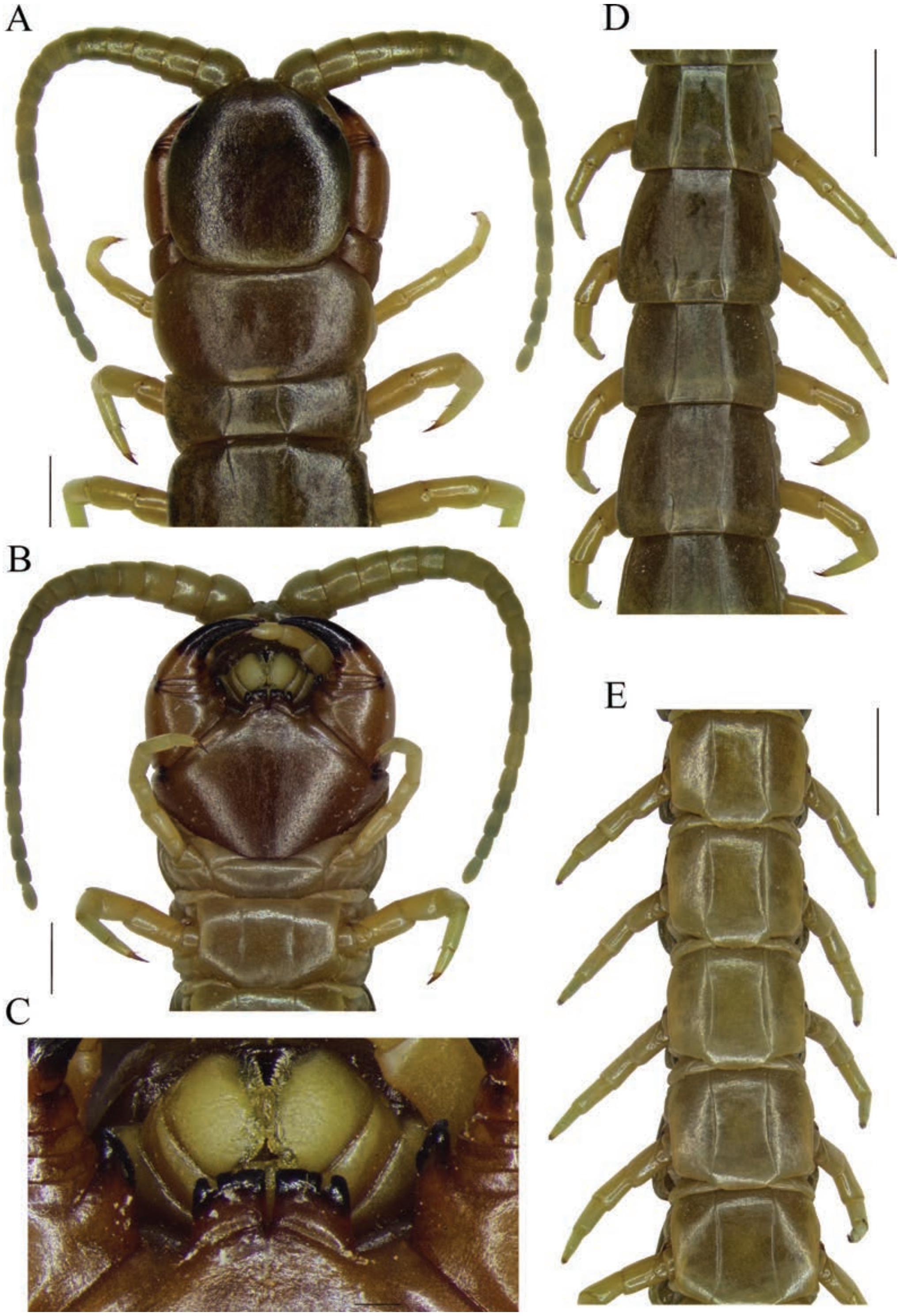


Figure 5. *Scolopendra chlorotes* neotype (= *S. oraniensis*); male; ("topotype 5", CEUAMr29) **A** cephalic plate, antennae, and TT1–3 **B** forcipular segment and sternites 1, 2 **C** tooth plates **D** tergites 10–14 **E** sternites 8–12. Scale bars: 0.2 mm (**C**); 1 mm (**A, B**); 2 mm (**D, E**).

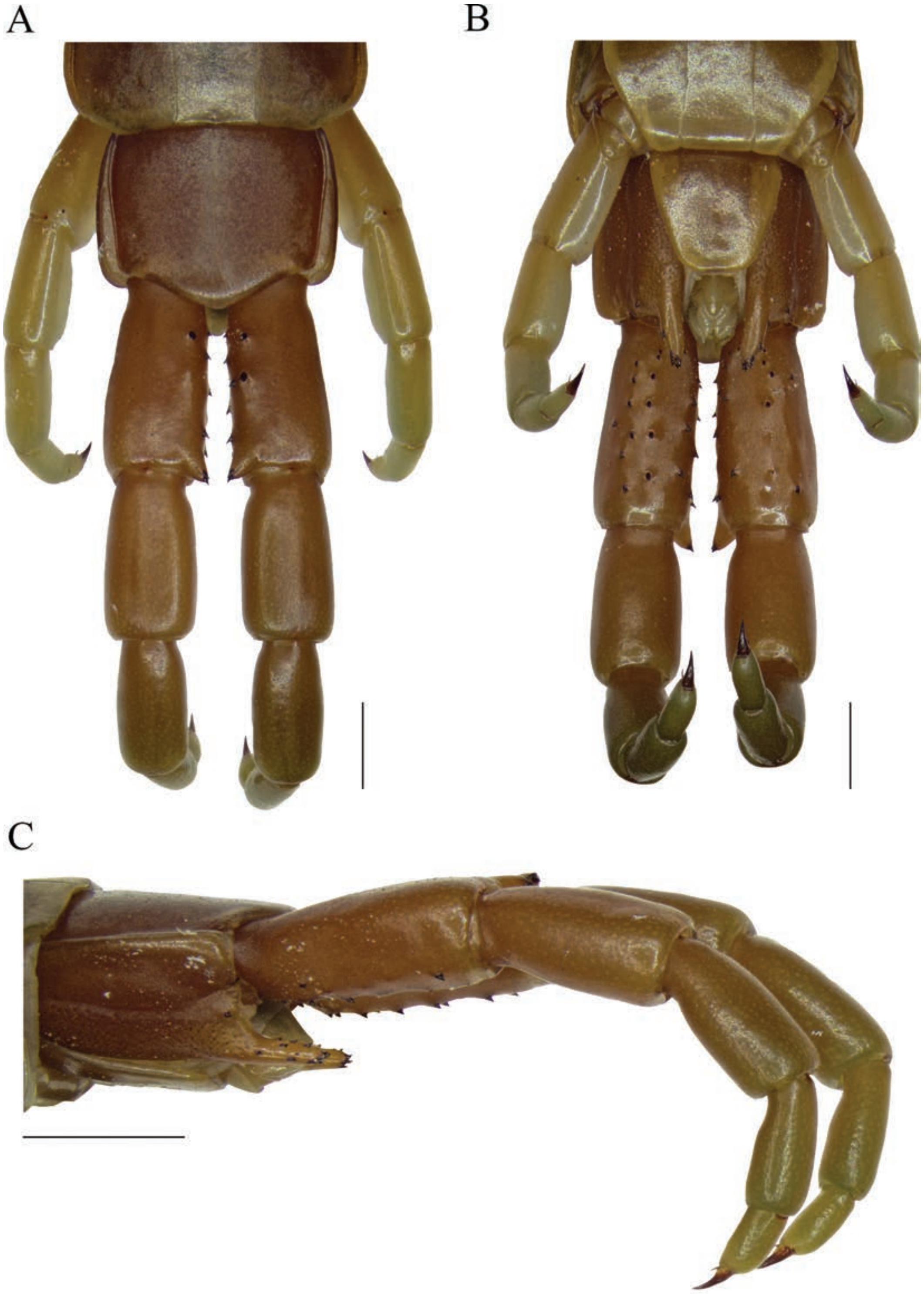


Figure 6. *Scolopendra chlorotes* neotype (= *S. oraniensis*); male; ("topotype 5", CEUAMr29) **A** ULBS's and UL's dorsal view **B** ULBS's and UL's ventral view **C** ULBS's, coxopleuron, and UL's ventral lateral view. Scale bars: 1 mm (**A, B**); 2 mm (**C**).

Remarks involving the type series and type series depository. All attempts to locate the type series of *S. chlorotes* were unsuccessful; the curators in their four probable depositories (NHMN, NHMUK, ZMB, and FAU) found no samples in their collections (pers. comm. Aug. 2020 to Nov. 2021).

According to Rühm (1925) and Hessel (2000) the types of this species most probable depository should be the NHMUK, on the basis that in 1925 the Naturhistorische Gesellschaft (NHG), lacking financial resources, decided to move a large number of their specimens preserved in ethanol to the British Museum of Natural History. Nevertheless, the types of *S. chlorotes* are not registered nor found there.

The other smaller part of Koch's wet collection, probably containing this species type series, did remain at the NHMN. However, the NHG rooms, their catalogues, and a large part of the collections were damaged during World War II in 1945 and presumably also the *S. chlorotes* types (EM Neupert (NHG) pers. comm. Sep. 2020). Therefore, the type series of *S. chlorotes* is considered to be lost.

Original description comparison. Because the type material is unavailable, the features in the original description are compared to those of other Scolopendromorpha found in Peninsular Spain to determine to which taxon L. Koch was referring when he erected *S. chlorotes* as a new species (Table 2). In this case, the original description of *S. chlorotes* allows exclusion of all *Cryptops* species because the sternite sutures are cruciform or trigonal (rather than only the two paramedial ones) and the UL prefemoral spines and (most likely referred to as) coxosternal tooth plates are absent in this genus (Schileyko et al. 2020). Neither of the two Mediterranean representatives of the family Plutoniumidae match with the morphological description of *S. chlorotes* since both have sternites with a distinctive single medial longitudinal suture and none, or just one, spine on UL prefemur (Bonato et al. 2017b). The compatibility of *S. cingulata* is also rejected due to the absence of the longitudinal suture on the T21 with the incompatibilities in the prefemoral spinulation of the UL (Table 2). Furthermore, all of these taxa can be also ruled out because their colours do not match with those of *S. chlorotes* (Table 2).

Hence, its unambiguous morphology and colouration, compatible location, and the exclusion of all other Iberian Scolopendromorpha are facts that, combined, strongly suggest that if it is not the same taxon, the closest relative to *S. chlorotes* is *S. oraniensis* (Table 2).

Neotype and "topotypes" morphological comparisons. A total of fifteen *S. chlorotes* topotypical specimens were collected in five municipalities "near Málaga" (L. Koch 1856; Figs 2A, D, E, 5, 6; Suppl. material 1: file 3). All these specimens were examined and confirmed to be conspecific (Suppl. material 1: file 3). Among those, a neotype was selected (ICZN 1999: Art. 75; Figs 5, 6, Table 3, Suppl. material 1: file 3). The comparison of the neotype and the other "topotypes" with the seven syntypes of the closest taxon *S. oraniensis* demonstrated that all these specimens possess identical diagnostic morphological features (see diagnosis and redescription above; Table 3; compare Figs 5, 6 with Figs 7, 8) and therefore, both taxa should be considered to be the same species.

Additionally, the neotype of *S. chlorotes* and the other "topotypes" were compared with those of *S. viridipes*, and conspecificity was also confirmed (compare Figs 3, 4 with Figs 5, 6; Table 3). Consequently, *S. chlorotes*, *S. viridipes*, and *S. oraniensis* are considered a single taxon with three names (Figs 3–8; Table 3).

Taxonomic and nomenclatural status. As long as the taxon *S. chlorotes* L. Koch in Rosenhauer, 1856 is recognised as conspecific with *S. oraniensis* Lucas, 1846, the principle of priority indicates that the valid name of *S. chlorotes* is *S. oraniensis* (ICZN 1999: Art. 23.3). Hence, *S. chlorotes* is subjectively designated as an invalid name since it is here considered a junior synonym of *S. oraniensis* (ICZN 1999: Art. 23.3).

Table 2. The original descriptive morphology of *Scolopendra chlorotes* in comparison to other Scolopendromorpha species described in Peninsular Spain. **Bold letters** indicate compatible features in other species. * indicates common to the entire Scolopendromorpha, interpretable, or poorly differentiated feature. Nr^{pp}= Not reported, presence possible. NA= Information not available.

	Scolopendra chlorotes **L. Koch in Rosenhauer, 1856**	***S. cingulata*** **Latreille, 1829**	***S. oraniensis*** **Lucas, 1846**	***Cryptops (Cryptops) anomalans*** **Newport, 1844**	***C. (C.) hispanus*** **Brölemann, 1920**	***C. (C.) hortensis*** **s. s. (Donovan, 1810)**	***C. (C.) lobatus*** **Verhoeff, 1931**	***C. (C.) parisi*** **s. s Brölemann, 1920**	***C. (C.) trisulcatus*** **Brölemann, 1902**	***C. (Trygonocryptops) longicornis*** **(Ribaut, 1915)**	***C. (T.) similis*** **Machado, 1953**	***Plutonium zwierleini*** **Cavanna, 1881**	***Theatops erythrocephalus*** **(C. L. Koch, 1847)**
Presence in Malaga	**Present**	**Present**	**Present**	Nr^{pp}	**Present**	Nr^{pp}	Absent	Nr^{pp}	Nr^{pp}	**Present**	**Present**	**Present**	**Present**
Length (in mm)	**42.22** (20 lignes)	100-155	**40-65**	**20-40**	16-30	12-30	10-13.5	14-21	**15-35**	**27-38**	30	**50-80**	**20-45**
Colouration	**Head-plate, antenna and tergites, brownish-green, maxillipeds, last tergite and UL reddish brown, and legs yellowish proximally and greenish distally**	Tergites yellowish ended with black distal edge, legs and antenna yellow to orange	**Pale cream to dark green or brown with antenna and legs yellowish, greenish, bluish or reddish**	Pale yellow to reddish	Pale yellow to reddish	Reddish, sometimes pale yellow	Pale yellow to reddish	Reddish	Pale yellow	Pale yellow	Pale yellow	Pale reddish, legs and antennae usually yellowish	Pale yellow to reddish, cephalic plate and UL usually darker
Headplate shape*	**Oval**	**Oval**	**Oval**	**Oval**	**Oval**	**Oval**	**Oval**	**Oval**	**Oval**	**Oval**	**Oval**	**Oval**	**Oval**
Tooth-plate on coxosternum	**Present**	**Present**	**Present**	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	**Present**	**Present**
Tergites shape*	**Tergite sides straight, TT1-3 and 20 rounded anteriorly**	**Quadrangular TT1-2 and T21 slightly smaller**	**Quadrangular TT1-2 and T21 slightly smaller**	**Quadrangular TT1-2 and T21 slightly smaller**	**Quadrangular TT1-2 and T21 slightly smaller**	**Quadrangular TT1-2 and T21 slightly smaller**	**Quadrangular TT1-2 and T21 slightly smaller**	**Quadrangular TT1-2 and T21 slightly smaller**	**Quadrangular TT1-2 and T21 slightly smaller**	**Quadrangular TT1-2 and T21 slightly smaller**	**Quadrangular TT1-2 and T21 slightly smaller**	**Quadrangular TT1-2 slightly smaller,** Segment 21 longitudinal enlarged	**Quadrangular TT1-2 slightly smaller,** Segment 21 longitudinal enlarged
TT's paramedian sutures	**TT2-20**	**TT2/3-20**	**TT2-20**	**TT2-20**	**Sutures weak, apparently present since T2**	**TT3, 4 or 5-20**	**TT2-20**	**TT2/3-20**	**TT2-20**	**TT2, 3 or 4-20**	**TT2-20**	**TT2-20**	**TT2-20**
Tergites margination*	**TT14-21**	**TT7/12-21**	**Complete from TT19-21**	**TT3-19**	NA	**TT3, 4 or 5-20***	NA	**NA**	**TT3-20**	**TT4-21**	**TT3-20**	T21	T21
Median longitudinal suture on the T21	**Present**	Absent	**Present**	**Presence observed variable;** T21 with a depression	NA	NA, probably absent; T21 with a depression	NA, probably absent	Absent	**Present**	Absent	NA	**Present**	**Present**
Paramedian sutures on sternites	**Longitudinal, absent in S 21**	**SS2-20**	**SS2-20**	Cruciform sutures	Cruciform sutures	Cruciform sutures	Cruciform sutures	Cruciform sutures	Cruciform sutures	Trigonal sutures	Trigonal sutures	Single medial longitudinal suture	Single medial longitudinal suture
UL's prefemoral process	**Short, with two blunt spines at the extreme**	**Short, with 3-5 spines**	**Short, with 2 or 3, rarely up to 6 spines**	Absent	Absent (femur and tibia with 4 distal processes)	Absent	Absent	Absent	Present, with a single spine (femur with a distal process)	Absent	Present, with a single spine (femur with a distal process, tibia with distal two processes)	Process absent	Process absent
UL's spinous prefemoral formula	**V: 19 spines arranged in for rows, M:7 spines**	VL:0; V: 2; VM: 0; M: (1)2; DM: (1)2	**VL:3-5; V: 3-6; VM: 2-6; M: 4-8; DM:2-4**	Prefemur with setae, spines absent,7-10 saw teeth on tibia and 3-5 on tarsus 1	Prefemur with setae, spines absent, 8 saw teeth on tibia and 4 on tarsus 1	Prefemur with setae, spines absent, 5-8(9) saw teeth on tibia and 2-4 on tarsus 1	Prefemur with setae, spines absent, 6-10 saw teeth on tibia and 4-6 on tarsus 1	Prefemur with setae, spines absent, 6-12 saw teeth on tibia and 4-8 on tarsus 1	Prefemur with setae, spines absent, 13 saw teeth on tibia and 4 on tarsus 1	Prefemur with setae, spines absent, 12-13 saw teeth on tibia and 5 on tarsus 1	Prefemur with setae, spines absent, 10 saw teeth on tibia and 3 on tarsus 1	Spines absent	With one ventromedial prefemoral and one femoral spine

Scolopendra oraniensis **Lucas, 1846**

Types: Figs 7, 8; Table 3. Non-types: Figs 1C–I, 2B, D, 3–9; Tables 1–3; Suppl. material 1: files 1, 3

Scolopendra viridipes Dufour, 1820; nomen oblitum; senior syn. nov.
S. oraniensis Lucas, 1846; nomen protectum.
S. chlorotes L. Koch in Rosenhauer, 1856; junior syn. nov.
S. mediterranea Verhoeff, 1893: 318.
S. mediterranea lusitanica Verhoeff, 1893: 318.
S. clavipes Silvestri, 1897: 7 (sic.).
S. oraniensis africana Attems, 1902: 556.
Rhadinoscytalis canidens oraniensis: Attems 1926: 246.
S. canidens oraniensis: Attems 1930: 19, 36, 37, fig. 50.
S. canidens lusitanica Verhoeff, 1931: 309.
S. oraniensis: Würmli 1980: 348–350.

Morphological diagnosis [based on *S. oraniensis* type series]. Body length up to 64 mm. 18 or 19 antennal articles; 5½ basal ones glabrous in their entire surface. Antennae/cephalic plate length ratio ≈ 3.30. Forcipular trochanteroprefemoral process clearly defined, with two or three rather inconspicuous denticles. Tooth plate with 4+4 (rarely 3+3) teeth, divided into two groups. T1 without sutures or sulci. Paramedian sutures complete on tergites TT2–20. T21 with a complete median longitudinal suture. Margination starting at T14, complete on TT19–21. Sternite paramedian sutures on TT2–20. Coxopleuron basally pore-field, with a single medio-distal spine. Coxopleural process with a small pore-field, sub-cylindrical and quite elongated, with 9–14 spines altogether, disposed in sub/apical, dorsal, or lateral positions. Legs 3–20 with few setae. Two tarsal spurs on legs 1; a single tarsal spur on legs 2–18 or 19. Ultimate leg elongated, sometimes with a sinusoid transverse sulcus on the ventro-distal part; prefemoral spines (usually between 18–28) arranged in five frequently miss-aligned or duplicated rows with the VL: 1-5, V: 2-6, VM: 2-6, M: 4-8 and DM: 2-4 formula. Prefemoral process inconspicuous ending with two or three (rarely four) spines. Prefemur and femur of UL glabrous; tibia distally covered by sparse setae; tarsi 1 and 2 covered by small setae. UL/T21 length ratio ≈ 5.15.

Etymology. from the toponym "Oran", Algeria and the feminine (or masculine) suffix -*ensis* (from) meaning "from Oran", Algeria, in reference to the type locality.

Type series and type depository. Lucas (1846) did not declare on which specimens he based the nominal taxon of *S. oraniensis* (type series) (ICZN 1999: Art. 72.4.1), neither exposing the specimens' depository nor designating a holotype (ICZN 1999: Art. 72.1.1). Otherwise, Kraepelin (1904) indicated the presence of the types [syntypes] at the MNHN in writing "– [*Scolopendra*] *oraniensis* Lucas. – Algérie: envir. d'Oran [surroundings of Oran] (H. Lucas, 1849 [sic.]. Types)", without further data. Therefore, after the examination of the MNHN specimens and their labels (Figs 7, 8) (ICZN 1999: Art. 72.4.2), I conclude that the type series for the *S. oraniensis* nominal taxon was erected on the basis of seven syntypes, all of them unsexed adults (Table 3). Depository MNHN, Paris, France. Jar Number 282. Samples (Figs 7, 8A–C) and labels (Fig. 8D) separated in three different assay tubes (containing 2/2/3 specimens, respectively).

Collector and collection date. P. H. Lucas, during winter, between 1839 and 1842 (Lucas 1846).

Type locality and habitat from Lucas 1846: Ravines of the “Sauton’s” (sic.) [Santon] mountains and ravines between Oran and Mers-el-Kebir, Oran wilayah; Algeria (ICZN 1999: Recommendation 76A.2). Lapidicolous.

Distribution. Known from southern France (including Corsica), southern Italy (including Sardinia and Sicilia), Malta, Spain (including Balearic Islands), Portugal, Morocco, and Algeria. Introduced in Japan (Attems 1930; Würmli 1980; Bonato et al. 2017a).

Proposed new nomenclatural status. Nomen protectum.

Type series composite redescription (Table 3). ***Colouration*:** Colouration of specimens preserved in ethanol is toasted to pale yellow (Figs 7, 8A–C). According to Lucas (1846), colouration of living specimen was as follows [morphological traits are interpreted in brackets]:

(Original colour description available from: https://www.biodiversitylibrary.org/page/2362627#page/301/mode/1up)

Upper body part [anterior tergites] coppery black, lower [posterior tergites] green, in the middle ornamented with a yellowish green longitudinal stripe [probably, the translucence of the Malpighian tubule], [...] jaw [forcipules] reddish [...] palps greenish [second maxillae]; base of antenna green, in the middle greenish and in front stained dark red; feet [locomotory legs] green with dark red nails [unguis proper]; last pair of legs [UL] dark green [...].

Morphological description of the type series. [notes on brackets are comprehensive annotations from this text author]: Body length up to 64 mm. Antennae reaching up to T2 [maybe up to T3; actual length shrivelled by ethanol retraction]; with 18 or 19 articles, the basal 5½ ones dorsally and ventrally glabrous (Fig. 7A, B). Antennae/cephalic plate length ratio: 2.01 [reduced because of the antennae articles retraction caused by the preservation in ethanol; estimated to be ~ 3.30].

Cephalic plate with disperse puncta and a short anterior longitudinal depression; disto-median or/and paramedian sutures are absent. Posterior edge of cephalic plate overlapping the T1 (Fig. 7A). Coxosternal surface with disperse puncta, without sutures (Fig. 7B). Article 2 of second maxillary telopodite with spur. Forcipular trochanteroprefemoral process with one apical and two (rarely one) medial poorly differentiable teeth (Fig. 7C). Tooth plates slightly wider than tall, forming an obtuse angle (> 120°) with respect to the coxosternite; sensillae present. Each tooth plate with 4+4, rarely 3+3 teeth: the external one separated from the other three and inner ones sometimes fused. (Fig. 7C).

Spiracles triangular with three valves, present on body segments 3, 5, 8, 10, 12, 14, 16, 18, and 20.

T1 without sutures or sulcus (Fig. 7A); TT2–20 with complete paramedian sutures (Fig. 7D); T21 with a longitudinal median suture, surface of all tergites smooth, without depressions (Fig. 8A). T21 width/length ratio ≈ 1.35. Margination starting at T14, being complete in TT19–21.

Sternites with complete paramedian sutures from TT2–20 (Fig. 7E). Sternite of ultimate leg-bearing segment (Fig. 8B) with sides converging posteriorly; surface smooth, without depressions.

Coxopleuron not surpassing the posterior border of the tergite of the ULBS (Fig. 8B); with a dense pore-field area at the base and a single medio-distal spine. Coxopleural process sub-cylindrical and distinctly elongated, reaching up to the first 1/4 of the UL prefemoral length. The complete surface is covered by a loose pore-field with some small setae (Fig. 8C) and a total of 9–14 usually asymmetrically disposed spines; 4–6 of them in an apical/subapical position; 3–6 in a lateral position, and 1–3 in a dorsal position.

Leg 1 with two distal tarsal spurs on tarsus 1, one lateral anterior and one ventral; legs 1–18 or 19 (mode 19, Table 3) with only one ventral tarsal spur. Tibial spurs absent. Legs 1, 2, or 3 with or without isolated setae. Legs 3 or 4–20 with scarce setae.

UL moderately long and slender with ratios of lengths of prefemur and femur = 1.15, femur and tibia = 1.25, tibia and tarsus 2 = 1.80; tarsus 1 and tarsus 2 = 1.20 (Fig. 8C). Prefemora flattened dorsally, sometimes with a visible sinusoid transverse sulcus on the ventro-distal side (Fig. 8A, B). Spines are variable in number (total: 17–26) and size, usually arranged in five frequently asymmetrical, duplicate, and non-ordered rows, with a formula: VL: 3-6, V: 2-6, VM: 2-6, M: 3-8 and DM: 2-4. VM and M spine rows usually converging proximally; between them a flattened surface is present, regularly rounded proximally and without spines. Prefemoral process inconspicuously prominent, sometimes scarcely setose, ending with two, or rarely three, spines (Figs 8A–C). Setae on prefemur and femur almost absent, tibia distally scarce setose and tarsi 1 and 2 densely covered with short setae. UL/T21 length ratio ≈ 4.39 [reduced because of the retraction of the articles caused by the preservation in ethanol; ~ 5.15].

Genitalia retracted in the whole type series.

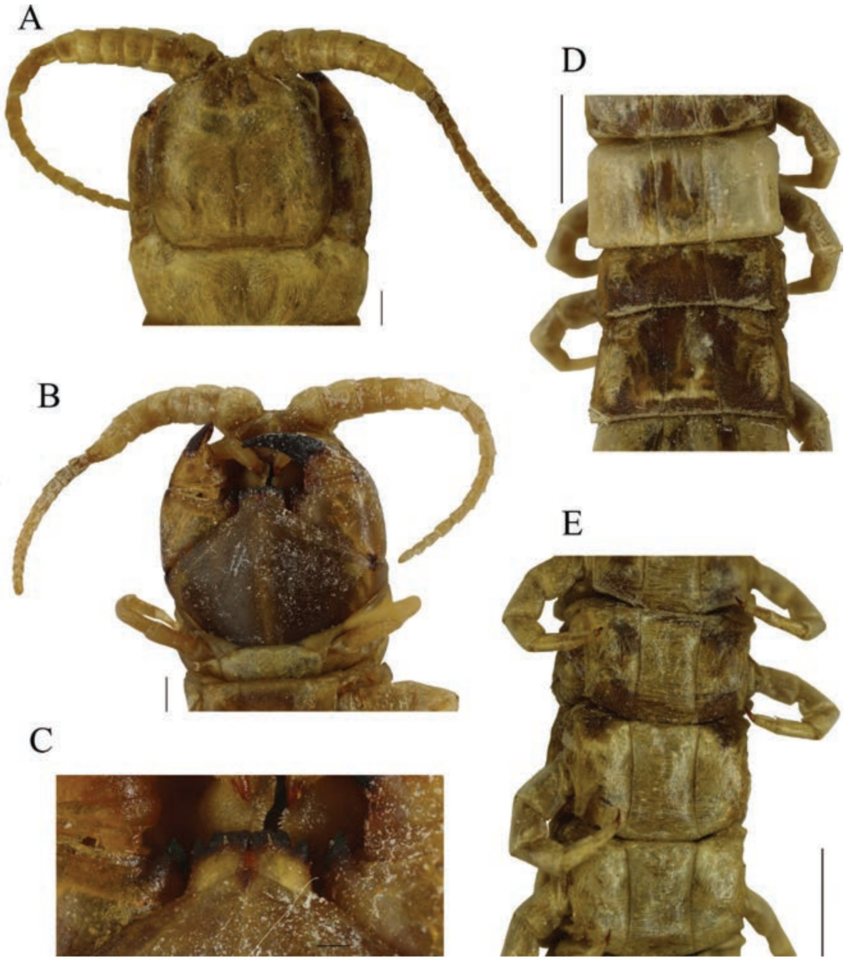


Figure 7. *Scolopendra oraniensis* syntype “1”; unsexed; (MNHN) **A** cephalic plate, antennae, and T1 **B** forcipular segment and sternites 1, 2 **C** tooth plates **D** tergites 3–6 **E** sternites 6–8. Scale bars: 0.2 mm (**C**); 1 mm (**A, B**); 2 mm (**D, E**).

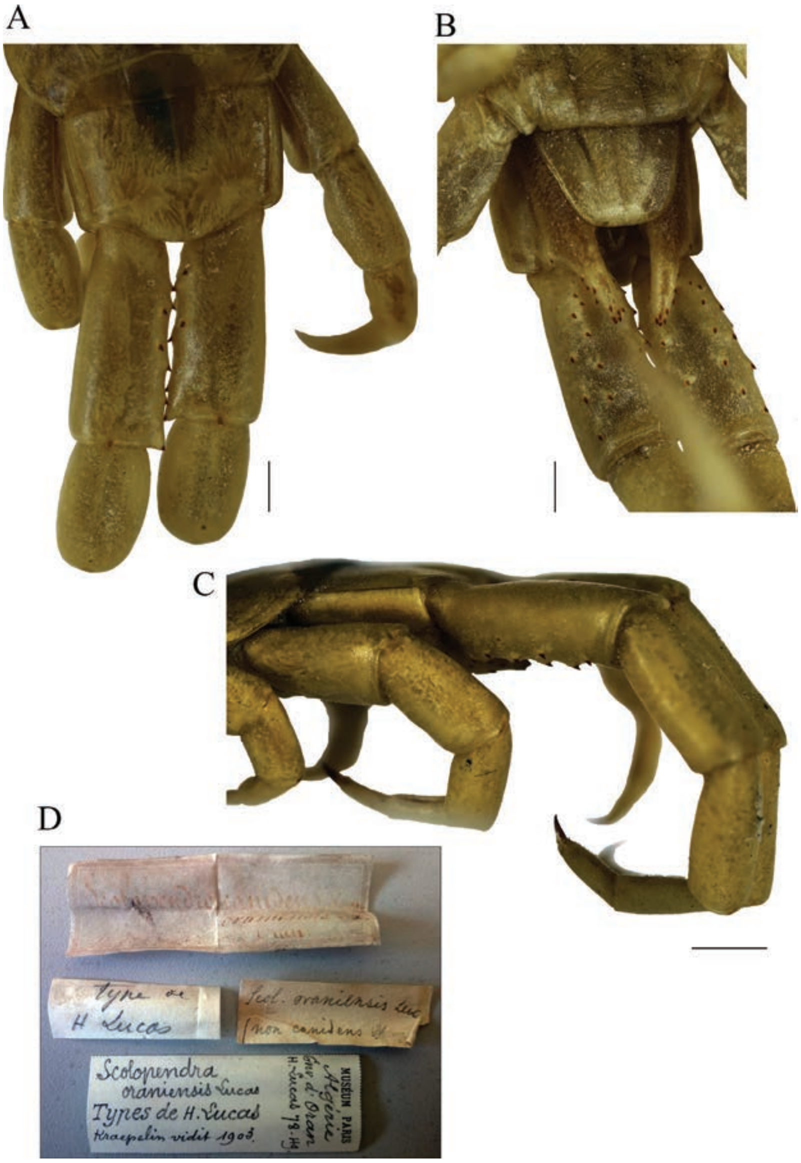


Figure 8. *Scolopendra oraniensis* syntype "1"; unsexed; (MNHN) **A** dorsal view of ULBS and UL **B** ventral view of ULBS and UL **C** lateral view of ULBS and UL **D** Original manuscript labels ordered chronologically. Top: old label [*Scolopendra canidens* Newp. *oraniensis* Luc. H. Lucas. [Leg.] Oran [type locality]; Middle: Kraepelin's 1903 labels ["Type de H. Lucas. *Scol*. *oraniensis* Luc. (non *canidens* Newp.)"]. Lower: MNHN staff "modern" summary label. Scale bars: 1 mm (**A, B**); 2 mm (**C**).

Genitalia description. (Based on *S. viridipes* and *S. chlorotes* "topotypical" material; Fig. 9A–D).

Genitalia well developed, reaching the apical part of coxopleural process when extended. Sternite and tergite of genital segment 1 (TGS and SGS I) convex and distally round, with a proximal median suture – distally attenuated – forming the vertex of a poorly angulated keel (Fig. 9A, B). In males (Fig. 9A) tergite of genital segment 2 (SGS II) small and horseshoe-shaped, with a poorly visible longitudinal suture. Gonopods short and small. Penis present, with fee endpoint, ventally serrated. TGS, SGS I, SGS II, lamina adanalis, gonopods and penis carrying scatted small setae, the remaining part of the genital structures glabrous. Sexual dimorphism or secondary sexual characteristics indistinct (Figs 9C, D); UL tibia and tarsi weakly and inconstantly more hirsute in females, with gender differences frequently indistinguishable.

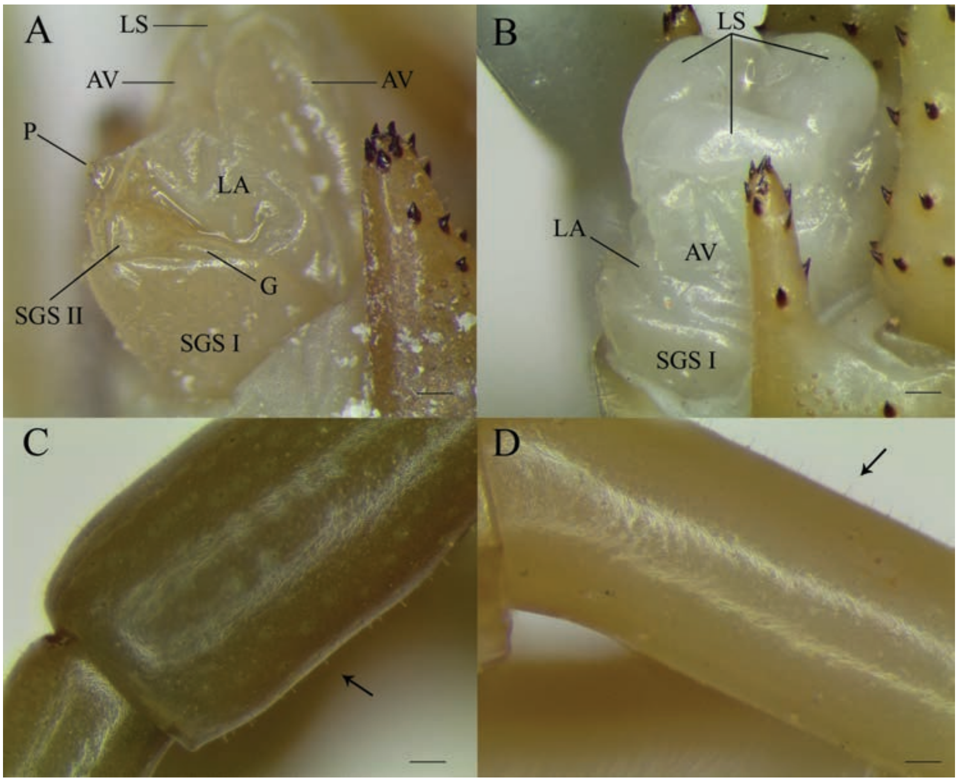


Figure 9. *Scolopendra oraniensis* genitalia **A** male (CEUAMr24); and **B** female (CEUAMr31), and detail of the setae (arrows) on tarsus 1 (**C, D)** on the same specimens **C** male and **D** female. Observe that on the contrary that Würmli (1980) indicated, the numbers of setae are actually similar in both genders. Legend: AV, anal valve; G. gonopod (folded back); LA, lamina adanalis; LS, lamina subanalis; P, penis; SGS I, sternite of genital segment 1; SGS II, sternite of genital segment 2. Scale bars: 0.1 mm.

Species variability. *Scolopendra oraniensis* has been observed to be somewhat variable in some few morphological features (Figs 3–9B; Table 3, Suppl. material 1: files 1, 3): number of antennal articles (17–20; mode 18–19), number of hirsute basal antennal articles (5–5½), number of teeth on tooth plates and on forcipular trochanteroprefemoral processes (respectively 3+3 vs 4+4; mode 4+4 and 3 vs 2; mode 3), beginning of complete margination of tergites (on TT17, 19, or 20; mode 17), tarsal spurs on leg 1 (0-2; mode 2), single tarsal spurs on legs (2–18 or 19; mode 2–19), coxopleural process morphology and UL prefemur number of spines (respectively 9–14 and 18–32), visibility of UL prefemoral ventro-distal horizontal suture, coxopleural and prefemoral process lengths or number of setae on the UL tarsi.

Additionally, the colouration has proven to be variable sympatrically (Figs 1D–I, 3–9). The cephalic plate and tergites can be monochromatic pale yellow to dark green/brown, sometimes reddish, sometimes with a darker/lighter longitudinal stripe. The forcipules can be yellowish to reddish, while the legs and antennae can be pale green, yellowish, bluish, reddish, or bicoloured, with occasional metallic reflections (Figs 1D–I, 3, 9).

These morphological and colouration characteristics, although tending towards a certain geographic distribution, often turn out to be variable within those populations (Table 3, Suppl. material 1: files 1, 3). Therefore, the separation of the species by their old names are clearly unjustified, since all the features can be explained by the known intraspecific variability of the taxon (Iorio and Geoffroy 2006; García-Ruiz 2018), which is also shared with many other species in the genus (Zalesskaja and Schileyko 1992; Siriwut et al. 2016; Doménech et al. 2018; Dyachkov and Nedoev 2021; Tsukamoto et al. 2021).

Differential diagnosis. Morphologically, *S. oraniensis* is related to five other species of the *S. canidens* group distributed around the Mediterranean Sea and Middle Asia (Würmli 1980; Simaiakis and Mylonas 2008). *Scolopendra clavipes* (Middle Asia) can easily be distinguished from *S. oraniensis* by the clavate morphology of the UL, while the two subspecies of *S. dalmatica* C. L. Koch, 1847 (northeastern Mediterranean) can be differentiated by their larger size (up to 80 mm), the incomplete median suture of T21, and the four spines of the UL prefemoral process. However, the morphologically closest relatives to *S. oraniensis* are *S. canidens* (southeastern and eastern Mediterranean) and *S. cretica* Lucas, 1853 (eastern Mediterranean, probably endemic to Crete, Greece). These two latter species can be unequivocally differentiated from *S. oraniensis* by the number of glabrous articles in the antennae (10–12 vs 5–5½, respectively), the type of transition between the glabrous/hirsute articles (gradual vs abrupt), and the number of spines in the prefemoral process (generally 3 vs 2 or 3). Between *S. canidens* and *S. cretica*, the only visible difference is the presence of brush-like setae in tarsi 1 and 2 of the UL in the *S. craetica* females (Würmli 1980; Lewis 2010; Dyachkov (ASU) pers. comm. 2022; Huesca pers. comm. 2018).

In these last two species closest to *S. oraniensis*, comparative analyses such as antennae/cephalic plates and T21/UL length ratios and their genitalia descriptions have not been performed yet.

Nomenclatural considerations. To verify the actual identities of *S. viridipes* and *S. chlorotes*, establishing the *S. oraniensis* specimens Lucas (1846) on which he based the type series was necessary, to have reference material with which to unambiguously compare new material (ICZN 1999: Preamble, Art. 13, Recomm. 13A). The *S. oraniensis* lectotype designation was found to be not nomenclaturally required (ICZN 1999: 11; point 6 in introduction; Art. 72.1.1; 74.7). However, neotypes designations for *S. viridipes* and *S. chlorotes* were mandatory to clarify their type localities and taxonomic situations in the absence of the original types (ICZN 1999: Art. 75, 76). Finally, the identities of *S. viridipes*, *S. chlorotes*, and *S. oraniensis* have been solved, and they are all conspecific (Figs 3–8; Table 3) leaving the name *S. oraniensis* Lucas, 1846 as nomen protectum with which to unambiguously refer to “all” of these species (ICZN 1999: Art. 23.3 and 23.9.2).

At a nomenclatural level, the specific epithet of *S. oraniensis* obviously conformed to the reference of the type locality (Gervais 1847). However, that noun is composed by the feminine (or masculine) suffix “*-ensis*” (coming from) and the prefix (a toponym) “Orani”, in the place of “Oran”. Coincidentally, “Orani” is the name of two other localities located in Italy and the Philippines. This can lead to etymological confusion, especially for the Italian Orani, on Sardinia, a region where *S. oraniensis* also lives (Würmli 1980; Bonato et al. 2017a). Therefore, it is thought to be an incorrect original spelling (ICZN 1999: Art. 32.4) and according to the author’s intention to honour Oran, Algeria, rather than Orani, Italy, the proper name for *S. oraniensis* should be amended as “*S. oranensis*”. However, ICZN (1999: Art. 32.5.1) clearly states that this supposition should not be adhered to since, in the original publication, “The […] use of an inappropriate connecting vowel is not to be considered inadvertent errors”. Therefore, despite being confusing or misspelled, this name must not be corrected as it is valid in its original spelling; *S. oraniensis*.

Table 3. *Scolopendra oraniensis* type series morphological comparison with *S. viridipes*' and *S. chlorotes*' topotypes (= *S. oraniensis*; composite data from Supplementary tables 1 and 2). AP, apical spines; SAP, subapical spines; DS, dorsal spines; LS, lateral spines; VL, ventro-lateral spines; V, ventral spines; VM, ventro-median spines; M, median spines; DM, dorso-median spiness; SP, prefemoral process spines; UL; ultimate legs, ULBS, ultimate leg-bearing segment; T, tergite; TT, tergites, S, sternite; SS, sternites, RG, Retracted genitalia; * No visible (cephalic plate flexed over firsts SS), interpretable or damaged.

	***Scolopendra oraniensis* (type series)**							***S. viridipes* (CEUAMr21-25)**	***S. chlorotes* (CEUAMr26-40)**
	Syntype “1"	**Syntype “2"**	**Syntype “3"**	**Syntype “4"**	**Syntype “5"**	**Syntype “6"**	**Syntype “7"**		
Body length in mm	64	60	58	52	42	41	41	35-40	26-60
Sex	RG	RG	RG, probably female	RG, probably female	RG	RG	RG	–	–
Antenna reaching to tergite*	T2*	T2*	T2*	T2*	T2*	T2*	T2*	T3	T3
Number of antennal articles	18/19	18/19	19/18	19/19	19/18	19/19	18/19	17-20	17-20
Number of proximal glabrous articles	5½	5½	5½	5½	5½	5½	5½	5	5-5½
Teeth on tooth plate	4+4	*	4+4	4+4	3+3	4+4	4+4	4+4	3+3; 4+4
Teeth on forcipular trochanteroprefemoral processes Total (apical /medial)	3(1/2) - 3(1/2)	*	3 (1/2) - 3 (1/2)	2 (1/1) - 3 (1/2)	2 (1/1) - 2 (1/1)	3(1/2) - 3(1/2)	3(1/2) - 3(1/2)	3(1/2)	2(1/1); 3(1/2)
Tergite paramedian sutures	TT2-20	TT2-20	TT2-20	TT2-20	TT2-20	TT2-20	TT2-20	TT2-20	TT2-20
Longitudinal suture on T21	Present	Present	Present	Present	Present	Present	Present	Present	Present
First tergite with complete margination	19	19	19	19	19	19	19	17-19	14-18
Paramedian sutures on sternites	SS2-20	SS2-20	SS2-20	SS2-20	SS2-20	SS2-20	SS2-20	SS2-20	SS2-20
Spines in coxopleuron (Left/Right)	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1
Spines in coxopleural process (Left/Right)	AP-SAP: 4/5 DS: 2/1 LS: 4/4 Total:10/10	AP-SAP: 5/4 DS: 2/1 LS: 4/4 Total:11/9	AP-SAP: 6/5 DS: 1/2 LS: 6/6 Total:13/13	AP-SAP: 5/6 DS: 3/2 LS: 6/4 Total:14/12	AP-SAP: 4/5 DS: 2/2 LS: 4/6 Total:10/12	AP-SAP: 6/5 DS: 3/2 LS: 3/4 Total:12/11	AP-SAP: 5/5 DS: 3/3 LS: 4/5 Total:12/13	AP-SAP: 4-8 DS: 1-3 LS: 2-3 Total: 7-14	AP-SAP: 4-7 DS: 0-4 LS: 1-4 Total: 5-15
Tarsal spurs on leg 1 (Left/Right)	2/2	2/2	2/1	2/2	2/2	2/2	2/2	0-2	1-2
Legs with one tarsal spur	2-19 (Left 1-18)	2-19	2-19	2-19 (Right 1-18)	2-19	2-19	2-19	2-19	2-18 or 19
Ultimate legs prefemoral spinulation and spines in prefemoral process (Left/Right)	VL:4/3 V: 6/6 VM: 4/4; M: 4/4; DM:2/2; SP:2/2; Total: 22/21	VL: 3/5; V: 3/5; VM: 5/6; M: 8/6; DM:4/4; SP:3/2; Total: 26/28	VL:1/3; V: 3/2; VM: 4/4; M: 5/5; DM:2/2; SP:3/4; Total: 18/20	VL:5/5; V: 5/4; VM: 3/2; M: 5/6; DM:2/2; SP:3/3; Total: 23/22	VL:4/5; V: 4/6; VM: 5/4; M: 4/6; DM:3/4; SP: 2/3; Total: 22/21	VL:6/5; V: 5/5; VM: 3/5; M: 3/6; DM:2/2; SP:2/2; Total: 21/25	VL: 3/5; V: 3/5; VM: 5/6; M: 6/6; DM:2/3; SP:3/2; Total: 22/27	VL: 3-7; V: 4-6; VM: 3-7; M: 5-8; DM: 2; SP: 2-3; Total: 19-33	VL: 2-10; V: 4-10; VM: 2-8; M: 2-10; DM: 1-7; SP: 0-5; Total: 11-50

Discussion

The identification of species that were described during the early time of binomial nomenclature (18th and 19th centuries) can often be a complicated task. The usually short and superficial descriptions as well as the frequent disappearance of type series are among the main reasons hindering these tasks. In that time, the limited access to information and collections, and the insufficient faunistic and taxonomic knowledge frequently caused the ignorance of some species names, or, on the contrary, the unintentional creation of many synonyms for the same taxon, with authors working individually in different countries with little or no communication. Since their description, the combination of these scenarios has affected the identities of *S. viridipes* and *S. chlorotes*.

After concluding on these species conspecificity with *S. oraniensis*, it can be observed that Lucas, when he described in 1846 his "greenish legged *Scolopendra*", he accidentally overlooked the legs colour similarity between his "new" species and Dufour's (1820) one, *S. viridipes*. Lucas certainly knew about the *S. viridipes* description (see Lucas 1840) when describing *S. oraniensis*, but either overlooked this taxon or maybe had a different interpretation of Dufour's text. On the other hand, both Dufour (1820) and L. Koch (1856) named their respective species, *S. chlorotes* and *S. viridipes*, highlighting the greenish colouration of the legs. Despite this similarity in colour and size, morphology and relatively close distribution, L. Koch did not realise that he was facing a previously described species. In this context, the creation of this synonym could be justified since none of L. Koch's previous literature supports the fact that this author was aware of the previous descriptions of *S. viridipes* or of *S. oraniensis*. Hence, the final result was that the same taxon was introduced under three different names.

Kraepelin (1903) accurately speculated about the identities of *S. viridipes*, *S. oraniensis*, and *S. chlorotes* when suggesting the probable synonymy of these three species. However, a remarkable transcription mistake in the *S. viridipes* description year "? *S. viridipes* Dufour, 1860 (sic.)" instead of 1820, probably caused this author to never question the priority of the name *S. oraniensis* as the actual senior name for this species (ICZN 1999: Art. 23). Since the reluctant treatment in Attems' work (1930), no other study involving these nomina inquirenda *S. viridipes* and *S. chlorotes* has been performed until now.

So far, the incorporation of molecular data has provided interesting insights in to the systematics of *Scolopendra* (Oeyen et al. 2014; Siriwut et al. 2015, 2016; Doménech et al. 2018; Tsukamoto et al. 2021). In this context, and with a few methodologically questionable exceptions (Siriwut et al. 2016; Kang et al. 2017), *Scolopendra* has constantly demonstrated a good correlation between morphology and the often-used biomarkers, despite geographic barriers, distances, and the well-known intraspecific morphological variations (Zalesskaja and Schileyko 1992; Siriwut et al. 2015, 2016; Doménech et al. 2018; Han et al. 2018; Dyachkov and Nedoev 2021; Tsukamoto et al. 2021). On the other hand, for *S. oraniensis* only four sequence of three distinct genes belonging to two specimens from Italy and Morocco, are currently available (Vathera et al. 2013; Oeyen et al. 2014). However, to completely rule out the existence of cryptic speciation, the *S. viridipes* and *S. chlorotes* neotypes and related materials used in this text could be included in a future molecular work which might support the current "old school" taxonomic outcomes obtained here.

Even in the absence of modern methodologies and since the present contribution has proven useful, other authors are encouraged to continue producing studies with this classic taxonomic approach. These endeavours could help to improve the current Chilopoda knowledge by clarifying the identity of some taxa described long ago, as it has been the case of *S. viridipes*, *S. oraniensis*, and *S. chlorotes*.

Acknowledgements

The author sincerely thanks S. Rojo (UA), V. M. Barberá (UA) and E. Larriba (UMH; Universitat Miguel Hernández, Elx, Spain) for their constructive comments on the manuscript. Also, thanks are extended to P. Gaboriaud (CLD),

J. J. Geoffroy and E. Leguin (MNHN), É. Iorio and L. Charles (SLB), G. Edgecombe and J. Beccaloni (NHMUK), J. Dunlop (ZMB), D. Cordes and E. M. Neupert (NHMN, FAU), B. Sánchez (MNCN), M. Meister (MZS), and M. A. Ferrández for providing valuable information about the types, type depositories, and other related taxa. Sincere acknowledgements are extended to A. Jouini (UPV), C. Kropf (NHMB), and to A. Ortiz for their respective interpretations of original descriptions. Thanks to A. Vercher, R. Perez, A. García, and A. Muñoz for helping in the logistics and collection of the "*S. viridipes*" and "*S. chlorotes*" topotypes and to M. Huesca, F. Rodríguez Luque (Faluke), D. Molina, J. Tizón, and to the NOAA/NWS staff for their permissions to use their pictures. Many thanks to Y. Dyachkov (ASU) and M. Huesca for the very valuable information provided in respect of *S. canidens* and *S. cretica*. Also thanks to R. Obregón (SAE) for the collecting permissions and to the staff of Generalitat Valenciana and Junta de Andalucía for the collecting permits. Thanks are also extended to J. B. Warren for the language corrections in the text. Additional thanks to the reviewers for their comments, which have improved the final version of this manuscript.

Finally, CD wishes to express his heartfelt gratitude to D. Cabanillas (UM; Universidad de Murcia, Spain) for his important and unselfish assistance, which has undoubtedly been critical to the completion of this work.

Additional information

Conflict of interest

The author has declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

No funding was reported.

Author contributions

The author solely contributed to this work.

Author ORCIDs

Carles Doménech https://orcid.org/0000-0003-1890-9434

Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

References

Attems C (1930) Myriopoda. 2. Scolopendromorpha. Das Tierreich. W. De Gruyter, Berlin and Leipzig 54, 308 pp. https://doi.org/10.1515/9783112373002

Bollman CH (1893) The Myriapoda of North America. Bulletin of the United States National Museum 46: 1–210. https://doi.org/10.5962/bhl.title.2787

Bonato L, Minelli A (2014) Chilopoda Geophilomorpha of Europe: A revised list of species, with taxonomic and nomenclatorial notes. Zootaxa 3770(1): 1. https://doi.org/10.11646/zootaxa.3770.1.1

Bonato L, Edgecombe GD, Lewis JGE, Minelli A, Pereira L, Shelley R, Zapparoli M (2010) A common terminology for the external anatomy of centipedes (Chilopoda). ZooKeys 69: 17–51. https://doi.org/10.3897/zookeys.69.737

Bonato L, Chagas A Junior, Edgecombe GD, Lewis JGE, Minelli A, Pereira LA, Shelley RM, Stoev P, Zapparoli M (2017a) ChiloBase 2.0. A World Catalogue of Centipedes (Chilopoda). http://chilobase.biologia.unipd.it [Accessed 10 Jan. 2020]

Bonato L, Orlando M, Zapparoli M, Fusco G, Bartolin F (2017b) New insights into *Plutonium*, one of the largest and least known European centipedes (Chilopoda): Distribution, evolution and morphology. Zoological Journal of the Linnean Society 180(4): 887–909. https://doi.org/10.1093/zoolinnean/zlw026

Brandt JF (1840) Observations sur les espèces qui composent le genre Scolopendra, suivies des charactères des espèces qui se trouvent dans le Muséum zoologique de l’ Académie des Sciences de St.-Petersbourg et de quelques coups d’ oeil sur leur distribution géographique. Bulletin Scientifique publié par l’Académie Impériale des Sciences de Saint-Pétersbourg 7(11): 147–160.

BV [Biodiversidad Virtual] (2024) Chilopoda. http://www.biodiversidadvirtual.org/ [accession: 21 Jan. 2024]

Cabanillas D (2019) Ampliación de la distribución de *Scolopendra cingulata* Latreille, 1829 y *Scolopendra oraniensis* Lucas, 1846 (Chilopoda, Scolopendromorpha, Scolopendridae) en la Comunidad de Madrid (España). Boletin de la Asociacion Espanola de Entomologia 43: 55–77.

Cabanillas D, García-Febrero O (2020) Primera cita de *Scolopendra cingulata* Latreille, 1829 (Scolopendromorpha: Scolopendridae) en las Islas Baleares (España). Boletin de la Asociacion Espanola de Entomologia 44: 203–206.

Cabanillas D, Parejo-Pulido D (2019) Primer registro de *Lamyctes* (*Lamyctes*) *emarginatus* (Newport, 1844) (Chilopoda: Lithobiomorpha: Henicopidae) en la Comunidad Autónoma de Extremadura y otras citas de la provincia de Badajoz (España). Boletin de la SEA 64: 307–311.

Cabanillas D, Albatros A, García-Ruiz A, Rodríguez-Luque F (2019) First observation of filial cannibalism in *Scolopendra cingulata* Latreille, 1829 (Chilopoda: Scolopendromorpha: Scolopendridae). Bulletin of the British Myriapod and Isopod Group 31: 26–33.

Carballo J, Daza JL (1991) Contribución al estudio faunístico de la clase Chilopoda en Andalucía occidental. Arquivos do Museu Bocage. Nova Série 2(5): 79–116.

Cavanna F (1881) Nuovo genere (*Plutonium*) e nuova specie (*P. zwierleini*) di Scolopendridi. Bollettino della Società Entomologica Italiana 13: 169–178.

Demange JM, Richard J (1969) Morphologie de l’appareil génital mâle des Scolopendromorphes et son importance en systèmatique (Myriapodes Chilopodes). Bulletin du Muséum National d’Histoire Naturelle 40: 968–983.

Di Z, Cao Z, Wu Y, Yin S, Edgecombe GE, Li W (2010) Discovery of the centipede family Plutoniumidae (Chilopoda) in Asia: A new species of *Theatops* from China, and the taxonomic value of spiracle distributions in Scolopendromorpha. Zootaxa 2667(1): 51–63. https://doi.org/10.11646/zootaxa.2667.1.4

Doménech C, Nagel P (2022) On the dates of publication of four European species of *Scolopendra* Linnaeus, 1758 described by C. L. Koch (Myriapoda, Chilopoda). Zootaxa 5159(1): 125–135. https://doi.org/10.11646/zootaxa.5159.1.6

Doménech C, Barberá VM, Larriba E (2018) A phylogenetic approach to the Philippines endemic centipedes of the genus *Scolopendra* Linnaeus, 1758 (Scolopendromorpha, Scolopendridae), with the description of a new species. Zootaxa 4483(3): 401–427. https://doi.org/10.11646/zootaxa.4483.3.1

Doménech C, Cabanillas D, Gilgado JD, Garcia L, Hernández-Corral J (2023) Contribución al conocimiento de los ciempiés, milpiés (Myriapoda: Chilopoda, Diplopoda) e isópodos terrestres (Crustacea: Oniscidea) de la Sierra de Aitana (Alicante, España). Arxius de Miscel·lània. Arxius de Miscel.Lania Zoologica 21: 129–149. https://doi.org/10.32800/amz.2023.21.0129

Dufour JML (1820) Description de dix espèces nouvelles ou peu connues d'Insectes recueillis en Espagne. Annales générales des sciences physiques 6: 307–317.

Dufour JML (1888) Souvenirs d'un savant français. A travers un siècle 1780–1865. J. Rothschild. Paris, 348 pp.

Dyachkov YV, Nedoev KK (2021) A contribution to the centipede (Chilopoda: Geophilomorpha, Scolopendromorpha) fauna of Uzbekistan and Turkmenistan. Ecologica Montenegrina 41: 41–50. https://doi.org/10.37828/em.2021.41.6

Ferrández MA (2020) Léon Dufour y las arañas de España. Mundo Artropodo 8: 47–60.

García-Ruiz A (1993) Contribución al conocimiento de los quilópodos de la provincia de Jaén: I Puerto de Despeñaperros. Boletin del Grupo Entomologico de Madrid 6: 27–32.

García-Ruiz A (2007) Estudio biométrico de *Scolopendra cingulata* Latreille, 1829 (Chilopoda, Scolopendromorpha). Boletin de la SEA 1(40): 542–544.

García-Ruiz A (2018) Contribución al conocimiento cavernícola de *Scolopendra canidens*, subsp. *oraniensis* (Lucas, 1846) (Myriapoda, Chilopoda). Monografías Bioespeleológicas 13: 13–16.

Gervais MP (1837) Etudes pour servir a l'histoire naturelle des Myriapodes. In Annales des Sciences Naturelles. série 2, Tome VII: 35–60. Ed. Crochard, Librairie-editeur, Paris.

Gervais MP (1847) Histoire naturelle des insectes. Aptères. Librairie encyclopédique de Roret, Paris, 623 pp.

Giribet G (2015) Orden Scolopendromorpha. Revista Ibero Diversidad Entomologica 30: 1–9. [Sociedad Española de Entomología]

Han T, Lee YB, Kim S-H, Yoon H-J, Park IG, Park H (2018) Genetic variation of COI gene of the Korean medicinal centipede *Scolopendra mutilans* Koch, 1878 (Scolopendromorpha: Scolopendridae). Entomological Research 48(6): 559–566. https://doi.org/10.1111/1748-5967.12331

Hessel B (2000) Dr. Karl Ludwig Christian Koch (8.11.1825 - 1.11.1908) Eine kurze Übersicht über das Leben und Wirken eines großen Nürnberger Naturforschers. Naturhistorische Gesellschaft Nürnberg e.V. 39–46.

ICZN (1999) International Code of Zoological Nomenclature. Fourth Edition. The International Trust for Zoological Nomenclature, London, UK. https://www.iczn.org/the-code/the-code-online/

Iorio É (2003) Morphologie externe des appareils génitaux mâle et femelle de la famille Scolopendridae (Chilopoda, Scolopendromorpha). Bulletin de Phyllie 16: 10–16.

Iorio É, Geoffroy JJ (2006) Contribution à la connaissance de *Scolopendra oraniensis* H. Lucas, 1846 (Chilopoda, Scolopendromorpha, Scolopendridae). Le bulletin d'Arthropoda 27: 48–51.

Iorio É, Geoffroy JJ (2008) Les scolopendromorphes de France (Chilopoda, Scolopendromorpha): identification et distribution géographique des espèces. Riviéra scientifique 91: 73–90.

Kang S, Liu Y, Zeng X, Deng H, Luo Y, Chen K, Chen S (2017) Taxonomy and identification of the genus *Scolopendra* in China using integrated methods of external morphology and molecular phylogenetics. Scientific Reports 7(1): 16032. https://doi.org/10.1038/s41598-017-15242-7

Koch CL (1836) Deutschlands Crustaceen, Myriapoden und Arachniden. Ein Beitrag zur deutschen Fauna. Herausgegeben von Dr. Herrich-Schäffer. 9tes Heft. F. Pustet, Regensburg: Manz, 90 pp.

Koch CL (1847) System der Myriapoden. In: Herrich-Schäffer L (Ed.) Kritische Revision der Insectenfauna Deutschlands. Pustet, Regensburg, 270 pp.

Koch L (1856). Myriapoda. In: Die Thiere Andalusiens. Rosenhauer WG (Ed.) Erlangen, 416 pp.

Kraepelin K (1903) Revision der Scolopendriden. Mitteilungen aus dem Naturhistorischen Museum in Hamburg 20(2): 1–276.

Kraepelin K (1904) Catalogue des scolopendrides des collections du muséum d'histroire naturelle de Paris. Bulletin du Muséum National d'Histoire Naturelle 26(10): 316–324.

Laboulbène M (1865) Liste de Travaux d'Entomologie Publiés de 1811 à 1864 Par M. Léon Dufour. Annales de la Société entomologique de France. Société entomologique de France 4(5): 216–252. https://doi.org/10.1080/00379271.1863.11755421

Lamarck (De) JBPA (1838) Histoire naturelle des animaux sans vertèbres: les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent; Tome cimquième. Arachnides, Crustacés, Annelides, Cirrihpedes. Deuxième Édition: revue et augmentée de notes présentant les faits nouveaux dont la science s'est enrichie jusqu'à ce jour; par mm. G. P. Deshayes et H. Milne Edwards. Ed. J. B. Baillière, Paris and London, 219 pp. https://doi.org/10.5962/bhl.title.23116

Lamarck (De) JBPA (1839) Histoire naturelle des animaux sans vertèbres: les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs families, leurs genres, et la citation des principales espèces qui s'y rapportent; Tome deuxième. Arachnides, Crustacés, Annelides, Cirrihpedes. Troisième Édition: revue et augmentée de notes présentant les faits nouveaux dont la science s'est enrichie jusqu'à ce jour; par mm. G. P. Deshayes et H. Milne Edwards. Ed. Meline, Cans et Compagnie, Bruxeles, 698 pp. https://doi.org/10.5962/bhl.title.46287

Latreille M (1829) Les Myriapodes. Le régne animal distribué d'après son organisation, Nouvelle Édition, Revue et Augmentée - Tome IV - Crustacés, Arachnides et Partie des Insectes. Cuvier. PML, Paris 4: 326–339.

Leach WE (1814) Crustaceology. In: Brewster D (Ed.) The Edinburgh Encyclopaedia. Balfour, Edinburgh 7 (2): 383–437.

Lewis JGE (2010) A key and annotated list of the *Scolopendra* species of the Old World with a reappraisal of *Arthrorhabdus* (Chilopoda: Scolopendromorpha: Scolopendridae). International Journal of Myriapodology 3(1): 83–122. https://doi.org/10.1163/187525410X12578602960380

Lewis JGE (2011) A review of the species in the genus *Cryptops* Leach, 1815 from the Old World related to *Cryptops* (*Cryptops*) *hortensis* (Donovan, 1810) (Chilopoda, Scolopendromorpha). International Journal of Myriapodology 4: 11–50. https://doi.org/10.3897/ijm.4.1116

Linnaeus C (1758) Systema naturae. Editio Decima. Laurentius Salvius: Holmiae, 824 pp.

Linnaeus C (1767) Systema Naturae per regna tria nature, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio duodecima, reformata - Laurentius Salvius. Holmiae 2: 533–1327. https://doi.org/10.5962/bhl.title.158187

Lucas PH (1840) Histoire naturelle des crustacés, des arachnides et des myriapodes. P. Duménil, Paris, 600 pp. https://doi.org/10.5962/bhl.title.44485

Lucas PH (1846) Note sur quelques nouvelles espèces d'insectes qui habitent les possessions francaises du Nord de l'Afrique. Revue Zoologique 9: 283–289.

Lucas PH (1853) Essai sur les animaux articulés qui habitent l'ile de Crète - Revue et Magasin de Zoologie Pure et Appliquée 5(2): 514–531.

Machado A (1953) Alguns miriápodes de Espanha. Archivos Instituto de Aclimaticion 1: 77–92.

Matic Z, Darabantu C (1968) Contributo alla conoscenza dei Chilopodi epimorfi (Chilopoda-Epimorpha) della fauna di Spagna. Memorie del Museo Civico di Storia Naturale di Verona 16: 127–135.

Minelli A (2011) Class Chilopoda, Class Symphyla and Class Pauropoda. In: Zhang, Z.-Q. (Ed.) Animal biodiversity: a higher level classification scheme and study of taxonomic richness. Zootaxa 3148(1): 157–158. https://doi.org/10.11646/zootaxa.3148.1.31

Moritz M, Fischer SC (1979) Die Typen der Myriapoden-Sammlung des Zoologischen Museums Berlin. 11. Chilopoda. Mitteilungen aus dem Zoologischen Museum in Berlin 55(2): 297–352. https://doi.org/10.1002/mmnz.4830550215

NOAA/NWS (2022) National Oceanic and Atmospheric Administration, National Weather Service (NOAA/NWS 2022) website. www.noaa.gov [Accessed Nov. 2022; reproduced and modified according their licenses and given personal instructions; 7th Dec. 2022]

Newport G (1844) A list of the species of Myriapoda order Chilopoda contained in the cabinets of the British Museum with synoptic descriptions of forty-seven new species. Annals & Magazine of Natural History 13(82): 94–101. https://doi.org/10.1080/03745484409442576

Oeyen JP, Funke S, Böhme W, Wesener T (2014) The evolutionary history of the rediscovered Austrian population of the giant centipede *Scolopendra cingulata* Latreille 1829 (Chilopoda, Scolopendromorpha). PLOS ONE 9(9): e108650. https://doi.org/10.1371/journal.pone.0108650

Pirotta R (1878a) Miriapodi. Annali del Museo Civico di Storia Naturale di Genova XI: 1877–1878. [G. Doria e R. Gestro, Genova.]

Pirotta R (1878b) I miriapodi del "Violante". Annali del Museo Civico di Storia Naturale di Genova 11: 397–410.

Ranzani C (1841) Rendiconto delle Sedunt dell' Imp. Academie delle Scienze Di Pietroburgo. Nuovi annali delle scienze naturali 5: 394–445.

Ribaut H (1915) Biospeologica XXXVI. Notostigmophora, Scolopendromorpha, Geophilomorpha. Archives de Zoologie Expérimentale et Générale 55: 323–346.

Rosenhauer WG (1856) Die Thiere Andalusiens nach dem resulte einer Reise. Ed. Verlag von Theodor Blaesing, Erlangen, 429 pp. https://doi.org/10.5962/bhl.title.66016

Rühm J (1925) Der Neurenberger Naturforscher Dr. Ludwig Koch. Ein Gedenktblatt zum seinem 100. Geburstage am 8 Nov. 1925. Naturhistorischen Gesellschaft zu Nürnberg, 13 pp.

Schileyko AA, Vathera V, Edgecombe GD (2020) An overview of the extant genera and subgenera of the order Scolopendromorpha (Chilopoda): A new identification key and updated diagnoses. Zootaxa 4825(1): 1–64. https://doi.org/10.11646/zootaxa.4825.1.1

Serra A (1981) Contribución al conocimiento de *Cryptops* (*Trigonocryptops*) *longicornis* Ribaut (Chilopoda Scolopendromorpha). Publicaciones del Departamento de Zoologia. Universidad de Barcelona 7: 47–50.

Serra A (1983) Els Scolopendrinae i els Theatopsinae (Chilopoda. Scolopendromorpha) de la Península Ibérica. Butlletí de la Institutició Catalana d'Historia Natural 49(5): 77–83.

Simaiakis S, Mylonas M (2008) The *Scolopendra* species (Chilopoda: Scolopendromorpha: Scolopendridae) of Greece (E-Mediterranean): a theoretical approach on the effect of geography and palaeogeography on their distribution. Zootaxa 1792(1): 39–53. https://doi.org/10.11646/zootaxa.1792.1.3

Siriwut W, Edgecombe GD, Sutcharit C, Panha S (2015) The centipede genus Scolopendra in mainland Southeast Asia: Molecular phylogenetics, geometric morphometrics and external morphology as tools for species delimitation. PLoS ONE 10(8): e0135355. https://doi.org/10.1371/journal.pone.0135355

Siriwut W, Edgecombe GD, Sutcharit C, Tongkerd P, Panha S (2016) A taxonomic review of the centipede genus Scolopendra Linnaeus, 1758 (Scolopendromorpha, Scolopendridae) in mainland Southeast Asia, with description of a new species from Laos. ZooKeys 590: 1–124. https://doi.org/10.3897/zookeys.590.7950

Tsukamoto S, Hiruta SF, Eguchi K, Liao JR, Shimano S (2021) A new amphibious species of the genus *Scolopendra* Linnaeus, 1758 (Scolopendromorpha, Scolopendridae) from the Ryukyu Archipelago and Taiwan. Zootaxa 4952(3): 465–494. https://doi.org/10.11646/zootaxa.4952.3.3

Vadell M (2013) *Cryptops* (*Cryptops*) *lobatus* Verhoeff, 1931 (Chilopoda: Scolopendromorpha: Cryptopidae), primera cita para la península ibérica. Boletin de la Asociacion Espanola de Entomologia 37: 1–2.

Vathera V, Edgecombe GD, Giribet G (2013) Phylogenetics of scolopendromorph centipedes: Can denser taxon sampling improve an artificial classification? Invertebrate Systematics 27(5): 578–602. https://doi.org/10.1071/IS13035

Verhoeff KW (1931) Über europäische *Cryptops*-Arten. Zoologische Jahrbucher. Abteilung fur Systematik, Ökologie und Geographie der Tiere 62: 263–288.

Verhoeff KW (1934) Beiträge zur Systematik und Geographie der Chilopoden. Zoologische Jahrbucher. Abteilung fur Systematik, Ökologie und Geographie der Tiere 66(1/2): 1–152.

Voigtländer K, Reip HS (2013) Morphological, taxonomical and ecological contributions to the chilopod fauna of Andalusia (Sierra de Grazalema and Los Alcornocales), Spain. Graellsia 69(2): 217–241. https://doi.org/10.3989/graellsia.2013.v69.088

Walckenaer CA, Gervais MP (1844) Histoire naturelle des insectes. Aptères. Tome Quatrième. Librairie encyclopédique de Roret, Paris, 623 pp. https://doi.org/10.5962/bhl.title.61095

Würmli M (1980) Statistische Unterschungen zur Systematik und postembryonalen Entwicklung der Scolopendra canidens Gruppe (Chilopoda: Scolopendromorpha). Sitzungsberichte der Österreichischen Akademie der Wissenschaften 189: 315–353.

Zalesskaja NT, Schileyko AA (1992) The Distribution of Scolopendromorpha in the USSR (Chilopoda). Berichte des Naturwissenschaftlichen-Medizinischen Verein Innsbruck 10: 367–372.

Supplementary material 1

Supplementary information

Authors: Carles Doménech

Data type: docx

Explanation note: **file 1.** *Scolopendra viridipes* (=*S. oraniensis*) neotype and “topotypes” morphological comparisons. AP, apical spines. SAP, subapical spines. DS, dorsal spines. LS, lateral spines. VL, ventro-lateral spines. V, ventral spines. VM, ventro-median spines. M, median spines. DM, dorso-median spines. SP, prefemoral process spines. UL, ultimate legs. ULBS, ultimate leg-bearing segment. T, tergite. TT, tergites. S, sternite. SS, sternites. RG=Retracted genitalia. *= Not visible, damaged, or regenerated. **file 2.** List of references satisfying the second requisite of reversal precedence of the principle of priority (ICZN 1999: Art. 23.9.1.2), concerning the names S. viridipes Dufour, 1820 and S. oraniensis Lucas, 1846. **file 3.** *Scolopendra chlorotes* neotype (= *S. oraniensis*) and “topotypes” morphological comparison. AP, apical spines. SAP, subapical spines. DS, dorsal spines. LS, lateral spines. VL, ventro-lateral spines. V, ventral spines. VM, ventro-median spines. M, median spines. DM, dorso-median spines. SP, prefemoral process spines. UL, ultimate legs. ULBS, ultimate leg-bearing segment. T, tergite. TT, tergites. S, sternite. SS, sternites. RG, Retracted genitalia. SN, Supernumerary spines between VM and M rows. *= Not visible, damaged, or regenerated.

Link: https://doi.org/10.3897/zookeys.1208.122126.suppl1

ZooKeys 1208: 81–98 (2024)
DOI: 10.3897/zookeys.1208.127725

Research Article

Four new species of the genus *Camptoscaphiella* Caporiacco, 1934 (Araneae, Oonopidae) from Xizang, China

Xiaohan Wang[1], Yanfeng Tong[1], Shuqiang Li[2]

1 *College of Life Science, Shenyang Normal University, Shenyang 110034, Liaoning, China*
2 *Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China*
Corresponding author: Yanfeng Tong (tyf68@hotmail.com)

Academic editor: Yuri Marusik
Received: 17 May 2024
Accepted: 7 July 2024
Published: 26 July 2024

ZooBank: https://zoobank.org/64AFF550-64DD-4EBD-AEA5-2C38D0F6083A

Citation: Wang X, Tong Y, Li S (2024) Four new species of the genus *Camptoscaphiella* Caporiacco, 1934 (Araneae, Oonopidae) from Xizang, China. ZooKeys 1208: 81–98. https://doi.org/10.3897/zookeys.1208.127725

Abstract

Four new species of the genus *Camptoscaphiella* Caporiacco, 1934 are described from Xizang, China, i.e., *C. metok* Tong & Li, **sp. nov.** (♂), *C. shannan* Tong & Li, **sp. nov.** (♂♀), *C. trifoliata* Tong & Li, **sp. nov.** (♂♀) and *C. zayu* Tong & Li, **sp. nov.** (♂♀). Morphological descriptions, photographic illustrations and a distribution map of the four new species are given.

Key words: Aranei, biodiversity, goblin spiders, Himalaya, spider, taxonomy, Tibet

Introduction

The family Oonopidae is one of the most diverse spider families worldwide, comprising 115 extant genera and 1952 species, and 3 fossil genera and 45 species (WSC 2024). *Camptoscaphiella* Caporiacco, 1934 is a small genus, distributed mainly in montane tropical and subtropical regions in Asia, mostly within the Himalayan Plateau (WSC 2024). Baehr and Ubick (2010) revised this genus, with two species re-described and nine new species described from China, India, Nepal, Sri Lanka and Thailand, and a key to the known 15 species provided. Two other species were later recorded in the Pacific Island of New Caledonia (Baehr and Harvey 2013) and five species were documented from Yunnan, China (Huang et al. 2021; Wang et al. 2023). Altogether, 23 species have been recorded in the world (WSC 2024).

Up to now, seven species belonging to three genera of oonopid spiders have been recorded in Xizang of China (Cheng et al. 2021; Tong et al. 2023). Although there are no records of the genus *Camptoscaphiella* from Xizang, many species have been described from the adjacent areas, including one from Bhutan, three from India, seven from Nepal, and eight from Yunnan Province of China (Tong and Li 2007; Baehr and Ubick 2010; Huang et al. 2021; Wang et al. 2023).

In this paper, *Camptoscaphiella* is recorded for the first time from Xizang and four new species of the genus are described and photographed.

Materials and methods

The specimens were examined using a Leica M205C stereomicroscope. Details were studied under an Olympus BX51 compound microscope. Photos were captured with a Canon EOS 550D zoom digital camera (18 megapixels) mounted on an Olympus BX51 compound microscope. Endogynes were cleared in lactic acid. Scanning electron microscope (SEM) images were taken under high vacuum with a Hitachi S-4800 after critical-point drying and gold-palladium coating. All measurements were taken using an Olympus BX51 compound microscope and are in millimeters. The type material is deposited at the Shenyang Normal University (SYNU) in Shenyang, China.

The following abbreviations are used in the text and figures: **ALE** = anterior lateral eyes; **ap** = apodemes; **as** = anterior sclerite; **cd** = copulatory duct; **dp** = dorsal process; **mp** = median plate; **mpr** = median process; **np** = narrow process; **PLE** = posterior lateral eyes; **PME** = posterior median eyes; **pro** = prolateral outgrowth; **rlf** = retrolateral fold; **tfp** = trifurcate process; **tls** = thread-like structure; **vo** = ventral outgrowth; **vp** = ventral process; **wlo** = wing-like outgrowth.

Taxonomy

Family Oonopidae Simon, 1890

Genus *Camptoscaphiella* Caporiacco, 1934

Type species. *Camptoscaphiella fulva* Caporiacco, 1934, by monotypy.

Diagnosis. Males of this genus are similar to those of *Opopaea* Simon, 1892 in the extremely large, club-shaped palpal patella, but can be distinguished by the spination of the legs I–II (tibia I and II with four pairs of long spines, and metatarsus I and II with two pairs of long spines) vs. without spination; the cymbium not fused with the bulb vs. fused; and the reduced abdominal scuta vs. complete scuta. Females of this genus are similar to those of *Ischnothyreus* Simon, 1893, but can be separated by lacking the distinct, darkly sclerotized, strongly winding duct of endogyne and the uniquely shaped atrium.

Distribution. China (Xizang, Yunnan), South Asia (Bhutan, India, Nepal, Pakistan, Sri Lanka), Southeast Asia (Thailand) and New Caledonia.

Camptoscaphiella metok Tong & Li, sp. nov.

https://zoobank.org/4B0D244B-5E71-48DD-9D92-434C7A0B2AD1
Figs 1–2, 12

Material examined. ***Holotype*** China • ♂ (SYNU-1134); Xizang, Nyingchi, nr. Metok Co.; 29°19.382'N, 95°19.016'E, 980 m; 2.VIII.2013; Y. Lin leg.

Paratype: China • ♂ (SYNU-1135); same data as for holotype, Motuo Petrol Station; 22.IX.2013; Z. Gao leg.

Diagnosis. This new species is similar to *C. linyejiei* Tong & Li, 2021, but can be distinguished by their normal-sized eyes (Fig. 1B, G) vs. reduced (Huang et al. 2021: fig. 4B, G); and the thread-like structure (tls) on the tip of the psemblous (Fig. 2G, H), vs. lacking; and having a plate-like process (Huang et al. 2021: fig. 5G, H).

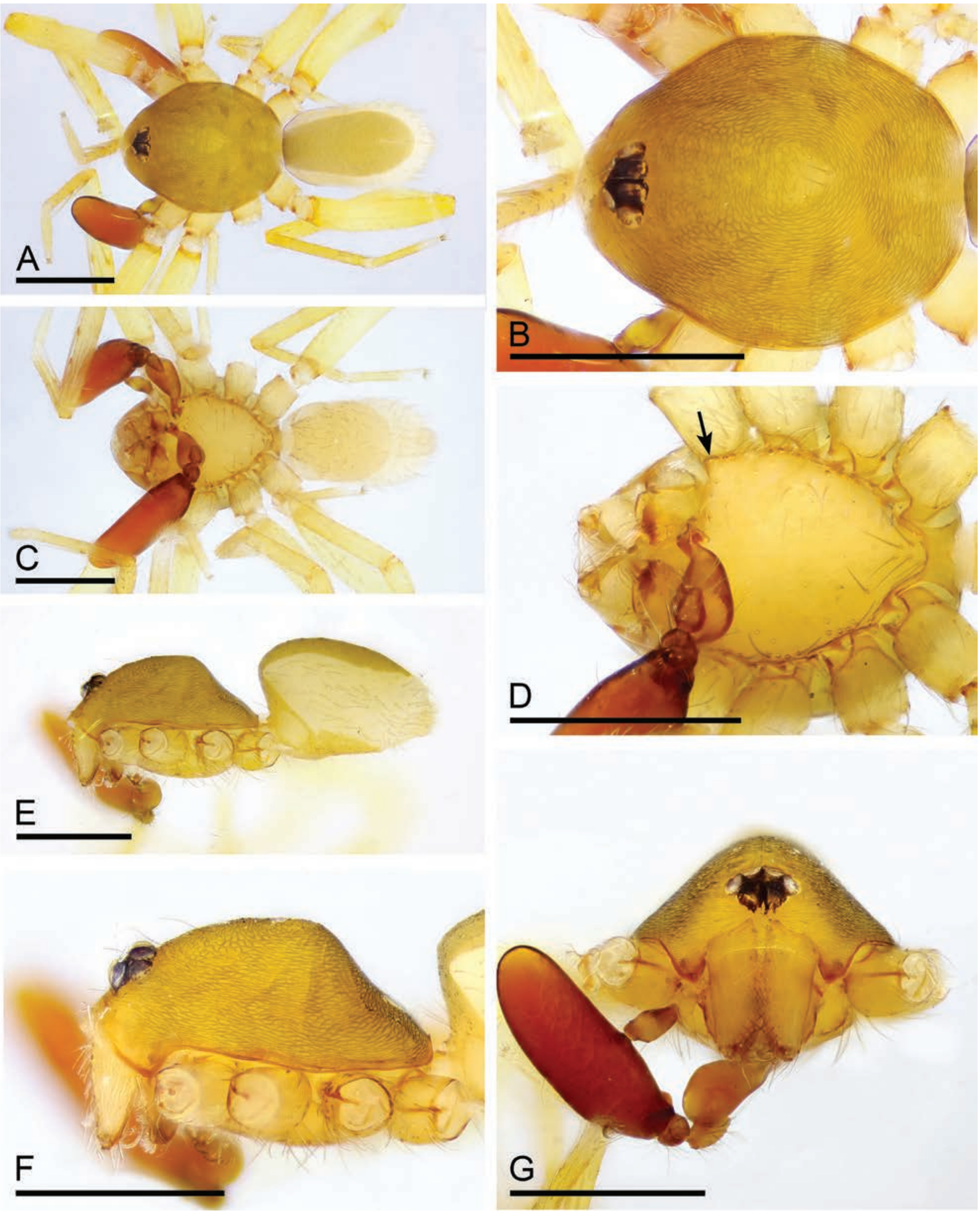


Figure 1. *Camptoscaphiella metok* sp. nov., male holotype **A, C, E** habitus, dorsal, ventral and lateral views **B, D, F, G** prosoma, dorsal, ventral, lateral and anterior views, arrow shows the pointed anterolateral bumps. Scale bars: 0.4 mm (**A–G**).

Description. Male (holotype). ***Body*:** uniformly colored, yellow; habitus as in Fig. 1A, C, E; length 1.29. ***Carapace*** (Fig. 1B, F): 0.66 long, 0.54 wide; pars thoracica strongly elevated in lateral view, entire surface finely reticulated. ***Eyes*** (Fig. 1B, G): ALE: 0.05; PME: 0.04; PLE: 0.04; ALE circular, PME oval, PLE oval;

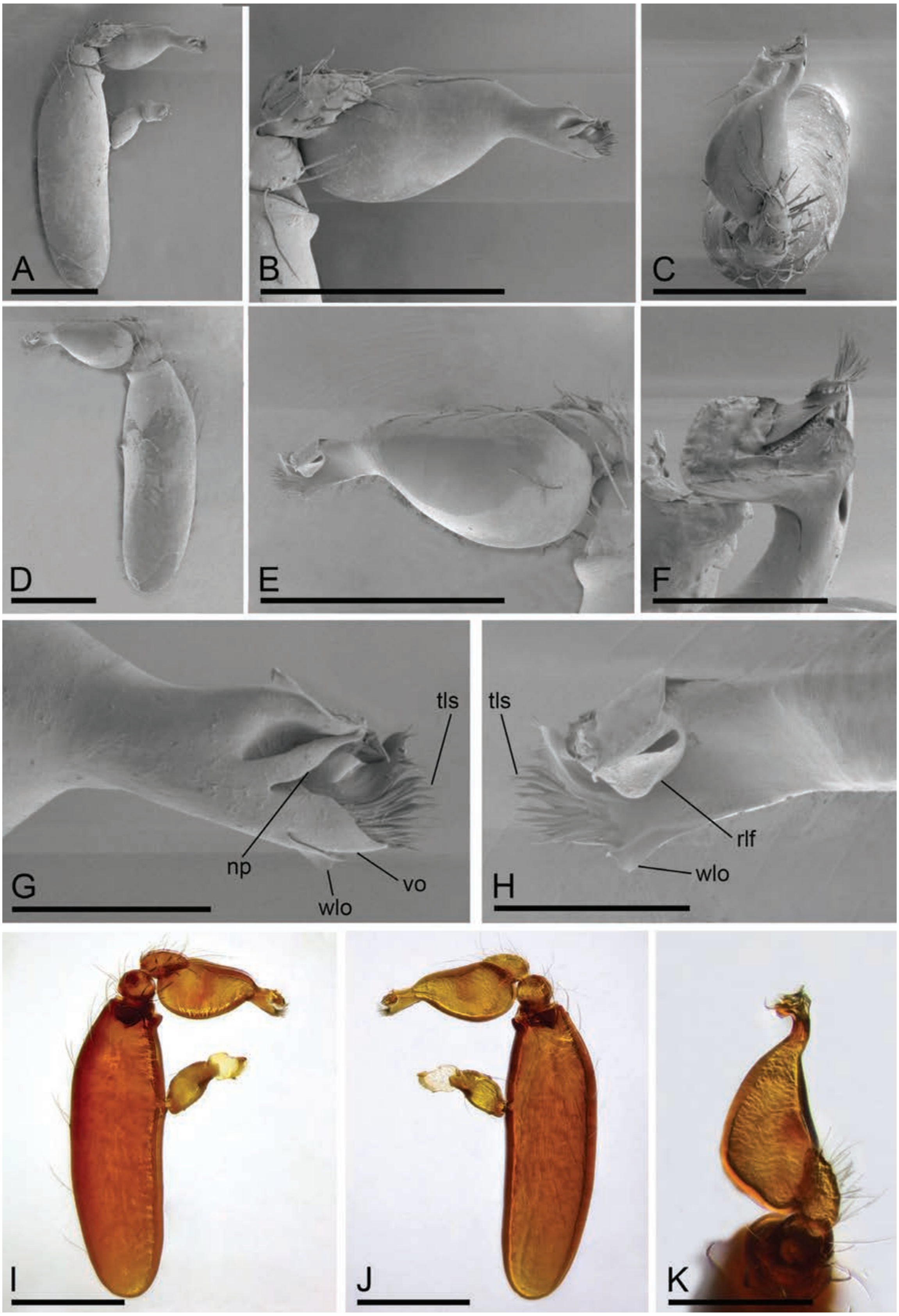


Figure 2. *Camptoscaphiella metok* sp. nov., male left palp **A, I** prolateral view **B, E** bulb, prolateral and retrolateral views **C, K** dorsal view **D, J** retrolateral view **F, G, H** distal part of bulb, dorsal, prolateral and retrolateral views. Abbreviations: np = narrow process; rlf = retrolateral fold; tls = thread-like structure; vo = ventral outgrowth; wlo = wing-like outgrowth. Scale bars: 0.2 mm (**A–E, I–K**); 0.05 mm (**F–H**).

posterior eye row procurved from both above and front; ALE separated by less than one radius. ***Clypeus*** (Fig. 1F, G): margin unmodified, straight in front view, sloping forward in lateral view. ***Mouthparts*** (Fig. 1D, G): chelicerae unmodified; anterior-median part of endites strongly sclerotized. ***Sternum*** (Fig. 1D): as long as wide, with pointed anterolateral bumps. ***Abdomen*** (Fig. 1A, C, E): 0.63 long, 0.34 wide; oval, scuta pale orange; dorsal scutum covering about 5/6 of abdomen length, about 3/4 of abdomen width, fused to epigastric scutum; postgastric scutum covering about 3/4 of abdominal venter. ***Palp*** (Fig. 2A–K): reddish brown; patella extremely long club-shaped, length/width = 3.04, about 5.6 times longer than femur, and 2.5 times longer than bulb; cymbium narrow (length/width = 1.68) in dorsal view; distal part of bulb with narrow process (np), broad ventral outgrowth (vo), a narrow wing-like outgrowth (wlo), a small retrolateral fold (rlf) and cluster of thread-like structure (tls).

Female. Unknown.

Notes. Seven species [*C. glenniei* (Fage, 1946) from India, *C. martensi* Baehr, 2010, *C. panchthar* Baehr, 2010, *C. silens* Brignoli, 1976, *C. strepens* Brignoli, 1976 and *C. taplejung* Baehr, 2010 from Nepal and *C. gunsa* Baehr, 2010 from India and Nepal] in adjacent areas are known only from females and this new species can be potentially conspecific with one of them.

Etymology. The specific name refers to the type locality and is a noun in apposition.

Distribution. Known only from the type locality.

Camptoscaphiella shannan Tong & Li, sp. nov.

https://zoobank.org/6EC89B40-CFA0-4E7C-8F75-9102C4BF40F3
Figs 3–5, 12

Material examined. ***Holotype*** China • ♂ (SYNU-1143); Xizang, Shannan City, Cona Co., Lemenba Ethnic Township, 17–20 km section from Lewang Bridge to Liulian Hwy; 27°47.700'N, 91°46.417'E, 3706 m; 5.VI.2016; J. Wu leg.

***Paratypes*:** China • ♀ (SYNU-1144); same data as for holotype • 6♀ (SYNU-1123–1128); same data as for holotype.

Diagnosis. The new species is similar to *C. tuberans* Tong & Li, 2007 and can be distinguished by the single strong bristle behind cheliceral paturons (Fig. 3D–H), vs. bristle absent (Tong and Li 2007: fig. 23); the strongly sclerotized median process (mpr) and a broad ventral outgrowth (vo) of the psembolus (Fig. 4D, H, K) vs. lacking the median process and having instead a very narrow, bifurcated ventral outgrowth (Tong and Li 2007: figs 25–27); and narrow forcipate median plate (mp) of endogyne (Fig. 5F, H) vs. circular median plate (Tong and Li 2007: fig. 22).

Description. Male (holotype). ***Body*:** uniformly colored, yellow; habitus as in Fig. 3A, C, E; length 1.83. ***Carapace*** (Fig. 3B, F): 0.81 long, 0.72 wide; pars thoracica slightly elevated in lateral view, entire surface finely reticulated. ***Eyes*** (Fig. 3B, H): ALE: 0.08; PME: 0.06; PLE: 0.06; ALE circular, PME oval, PLE oval; posterior eye row straight from above, procurved from front; ALE separated by less than one radius. ***Clypeus*** (Fig. 3F, H): margin unmodified, straight in front view, sloping forward in lateral view. ***Mouthparts*** (Fig. 3G, H): with single strong bristle behind paturons; anterior-median part of the endites strongly sclerotized. ***Sternum*** (Fig. 3D): as long as wide, with pointed anterolateral bumps.

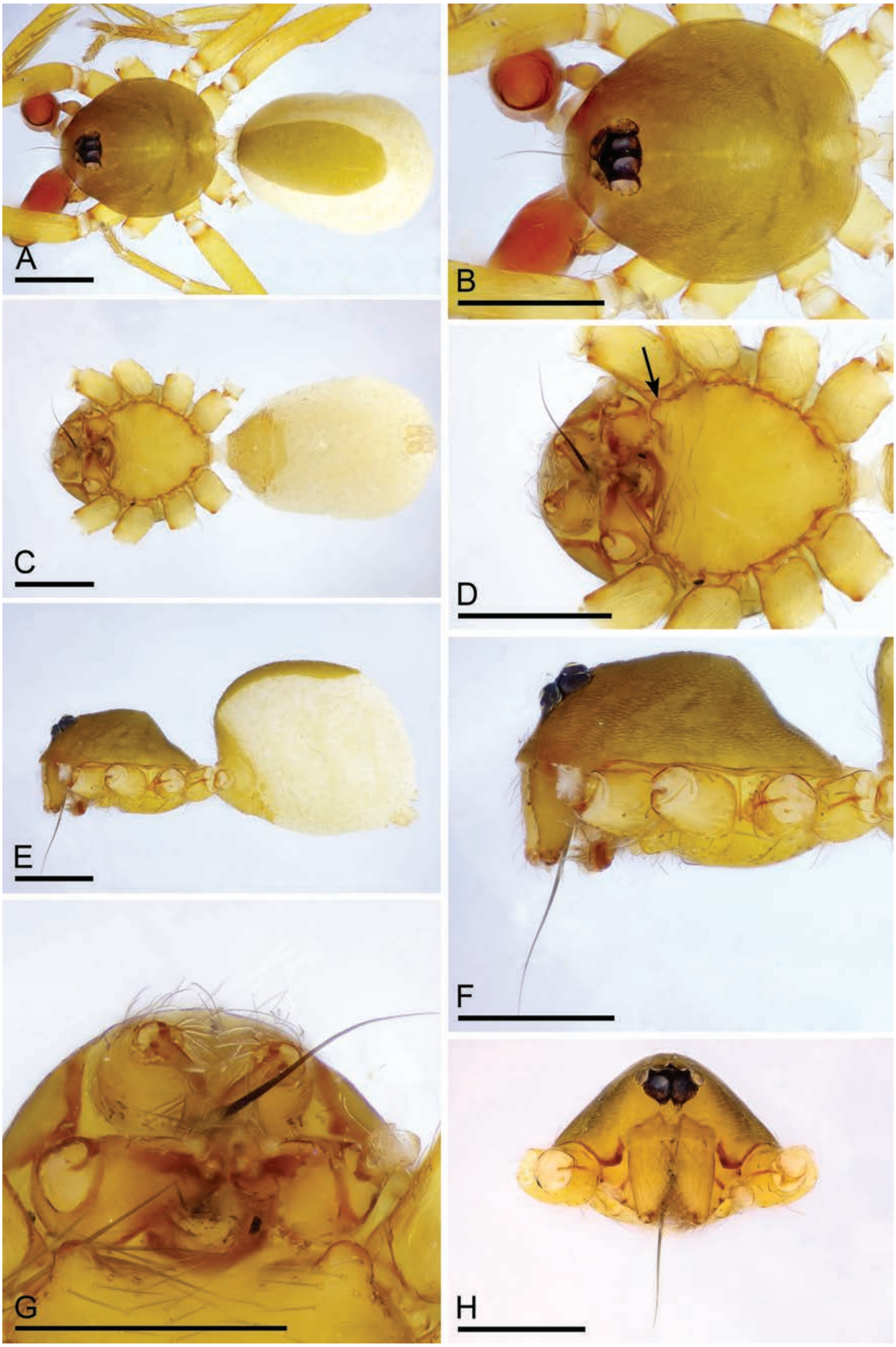


Figure 3. *Camptoscaphiella shannan* sp. nov., male holotype **A, C, E** habitus, dorsal, ventral and lateral views **B, D, F, H** prosoma, dorsal, ventral, lateral and anterior views, arrow shows the pointed anterolateral bumps **G** labium and endites, ventral view. Scale bars: 0.4 mm (**A–G**).

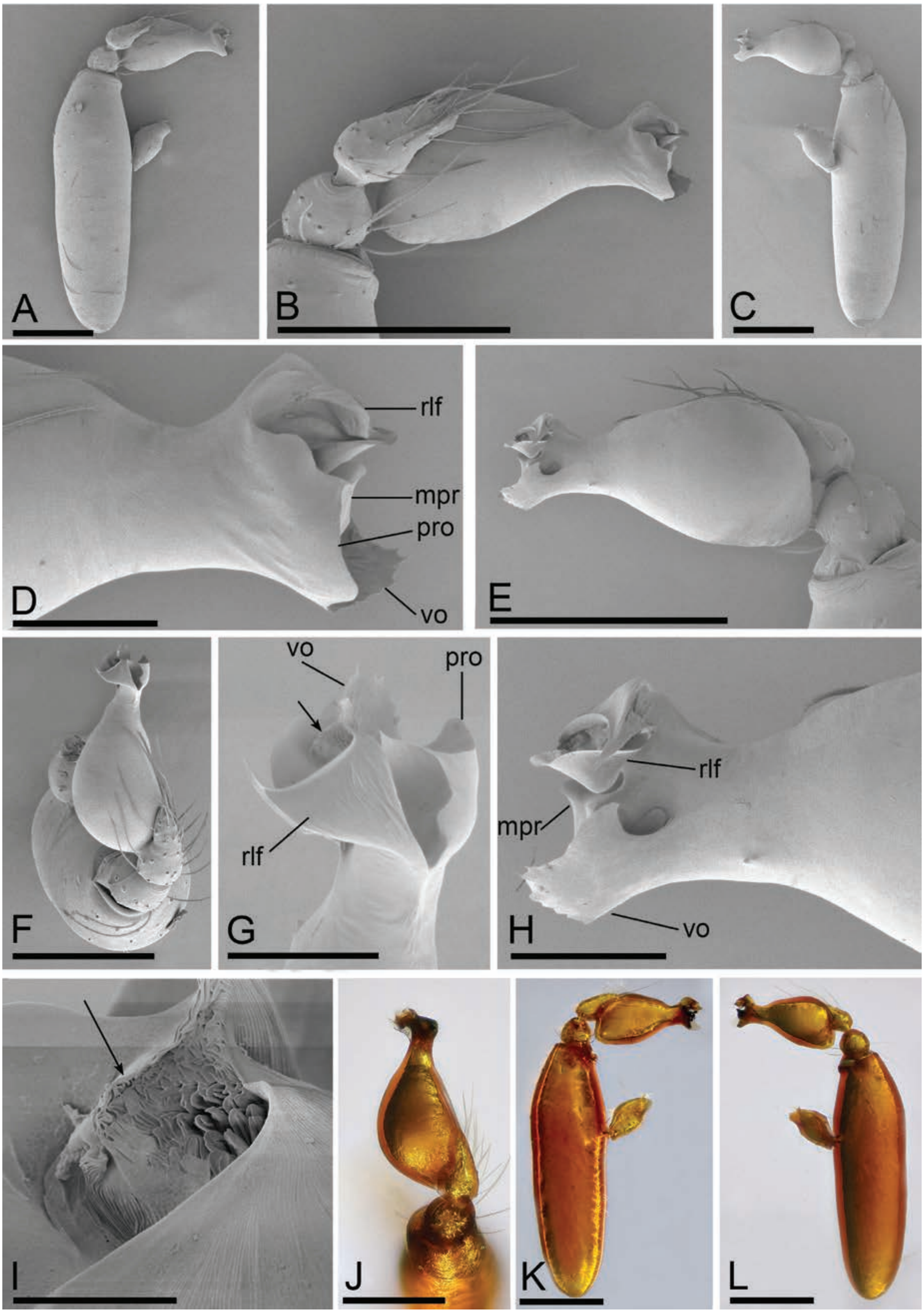


Figure 4. *Camptoscaphiella shannan* sp. nov., male left palp **A, K** prolateral view **B, E** bulb, prolateral and retrolateral views **C, L** retrolateral view **D, G, H** distal part of bulb, prolateral, dorsal and retrolateral views **F, J** dorsal view **I** same as **G** showing the details (arrow). Abbreviations: mpr = median process; pro = prolateral outgrowth; rlf = retrolateral fold; vo = ventral outgrowth. Scale bars: 0.2 mm (**A–C, E, F, J–L**); 0.05 mm (**D, G, H**); 0.01 mm (**I**).

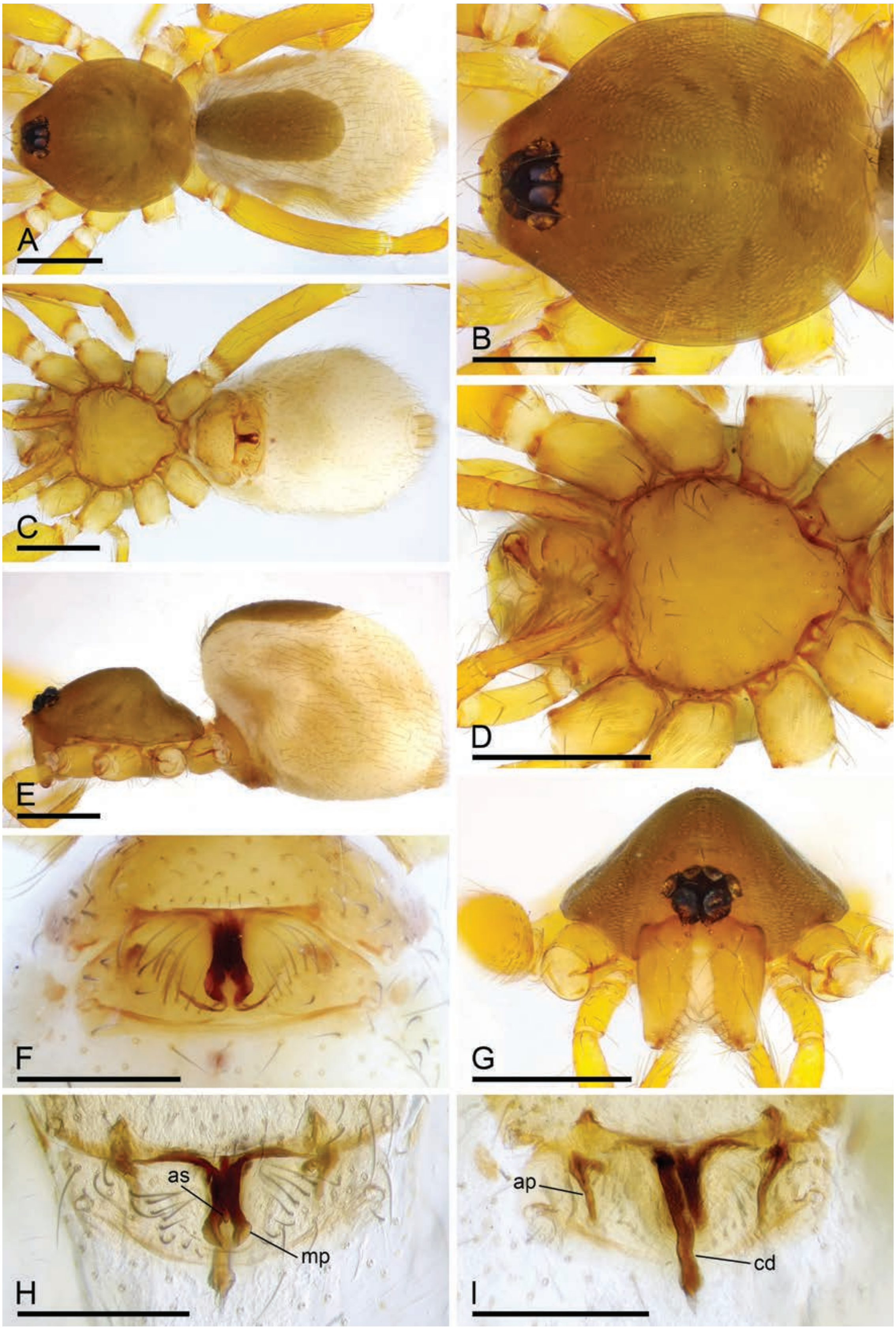


Figure 5. *Camptoscaphiella shannan* sp. nov., female paratype (SYNU-1144) **A, C, E** habitus, dorsal, ventral and lateral views **B, D, G** prosoma, dorsal, ventral and anterior views **F** epigastric region, ventral view **H, I** endogyne, ventral and dorsal views. Abbreviations: ap = apodemes; as = anterior sclerite; cd = copulatory duct; mp = median plate. Scale bars: 0.4 mm (**A–E, G**); 0.2 mm (**F, H, I**).

Abdomen (Fig. 3A, C, E): 1.02 long, 0.73 wide; oval, scuta pale orange; dorsal scutum covering about 2/3 of abdomen, 1/2 of abdomen width, fused to epigastric scutum; postgastric scutum small. ***Palp*** (Fig. 4A–L): reddish brown; patella extremely long club-shaped, length/width = 3.30, about 5.8 times longer than femur, and 3.2 times longer than bulb, cymbium narrow (length/width = 1.90) in dorsal view; psembolus with prolateral and ventral outgrowths (pro and vo respectively), strongly sclerotized median process (mpr) and small retrolateral fold (rlf).

Female (SYNU-1144). As in male except for the following. ***Body*:** habitus as in Fig. 5A, C, E; length 1.98. ***Carapace*:** 0.86 long, 0.73 wide. ***Eyes*:** ALE 0.07; PME 0.05; PLE 0.07. ***Abdomen*:** 1.12 long, 0.80 wide. Postgaster (Fig. 5F, H): with stick-like anterior sclerite (as) and forcipate median plate (mp). ***Endogyne*** (Fig. 5I): copulatory duct (cd) long, narrow, straight with tip well beyond postgastric scutum; apodemes (ap) short.

Etymology. The specific name refers to the type locality and is a noun in apposition.

Distribution. Known only from the type locality.

Camptoscaphiella trifoliata Tong & Li, sp. nov.

https://zoobank.org/C007206E-B7E4-46C9-A4F9-59DEE08A0442
Figs 6–8, 12

Material examined. ***Holotype*** China • ♂ (SYNU-1145); Xizang, Rikaze City, Jilong Co., Zalong Vill.; 28°22.865'N, 85°21.158'E, 2715 m; 31.VII.2014; Y. Li leg.

***Paratypes*:** China • 1 ♀ (SYNU-1100); Rikaze City, Dingjie Co., Chentang Town; 27°54.875'N, 87°28.869'E, 3267 m; 3.VIII.2014; Y. Li leg. • 1 ♂ (SYNU-1099); Rikaze City, Dingri Co., Rongxia Town; 28°03.450'N, 86°21.148'E, 3383 m; 27.VII.2014; Y. Li leg. • 2 ♂ (SYNU-1054–1055); Nyingchi, Bayi Distr., Bayi Town, Biri Mt; 28°51.334'N, 94°47.941'E, 2900 m; 11.VII.2013; Y. Lin leg. • 11♀ (SYNU-1057–1067); same data as above • 4♀ (SYNU-1146–1149); same data as above • 2 ♂ 4 ♀ (SYNU-1113–1118); Nyingchi, Bayi Distr., Lulang Town; 29°41.449'N, 94°43.605'E, 3530 m; 14.VII.2013; Y. Lin leg. • 9 ♂ 2 ♀ (SYNU-1101–1112); Nyingchi, Bayi Distr., Lulang Town; 29°21.449'N, 94°43.605'E, 3530 m; 14.VII.2013; Q. Cao leg. • 5 ♂ 1 ♀ (SYNU-1068–1073); Nyingchi, Mainling Co.; 29°13.310'N, 94°13.309'E, 3050 m; 13.VIII.2013; Y. Lin leg. • 2 ♂ 1 ♀ (SYNU-1152–1154); same data as above • 6 ♂ 4 ♀ (SYNU- 1074–1083); Nyingchi, Mainling Co.; 29°12.316'N, 94°12.649'E, 3060 m; 13.VIII.2013; Y. Lin leg. • 4♂10♀ (SYNU-1084–1097); Nyingchi, Mainling Co., Pai Town; 29°30.264'N, 94°53.868'E, 3321 m; 6.VIII.2015; J. Wu leg.

Diagnosis. Males of this new species are similar to those of *C. yujufeng* Tong & Yang, 2023, but can be distinguished by lacking a cluster of black, strong setae on the labium (Fig. 6D) vs. setae cluster present (Wang et al. 2023: fig. 5D) and psemblous with trifurcate process (tfp, Fig. 7D, K) vs. with semicircular, prolateral rim and trifurcate ventral process (Wang et al. 2023: fig. 6E, J). Females of the new species are similar to those of *C. zayu* sp. nov., but can be distinguished by the fusiform median plate (Fig. 8H) vs. pear-shaped (Fig. 11H) and the long copulatory duct, which extends beyond the postgastric scutum (Fig. 8I) vs. just reaching groove between posterior spiracles (Fig. 11I).

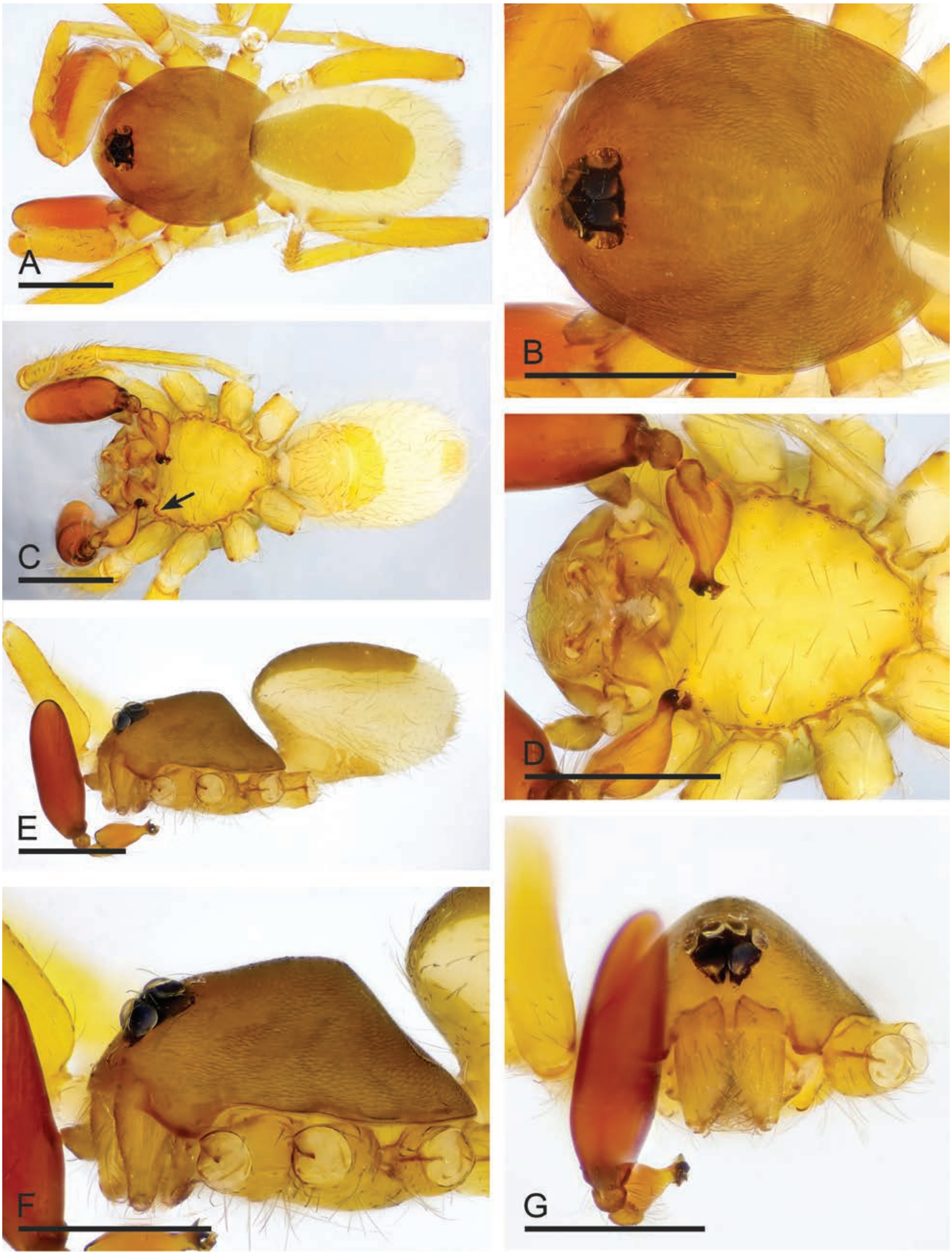


Figure 6. *Camptoscaphiella trifoliata* sp. nov., male holotype **A, C, E** habitus, dorsal, ventral and lateral views, arrow shows the pointed anterolateral bumps **B, D, F, G** prosoma, dorsal, ventral, lateral and anterior views. Scale bars: 0.4 mm (**A–G**).

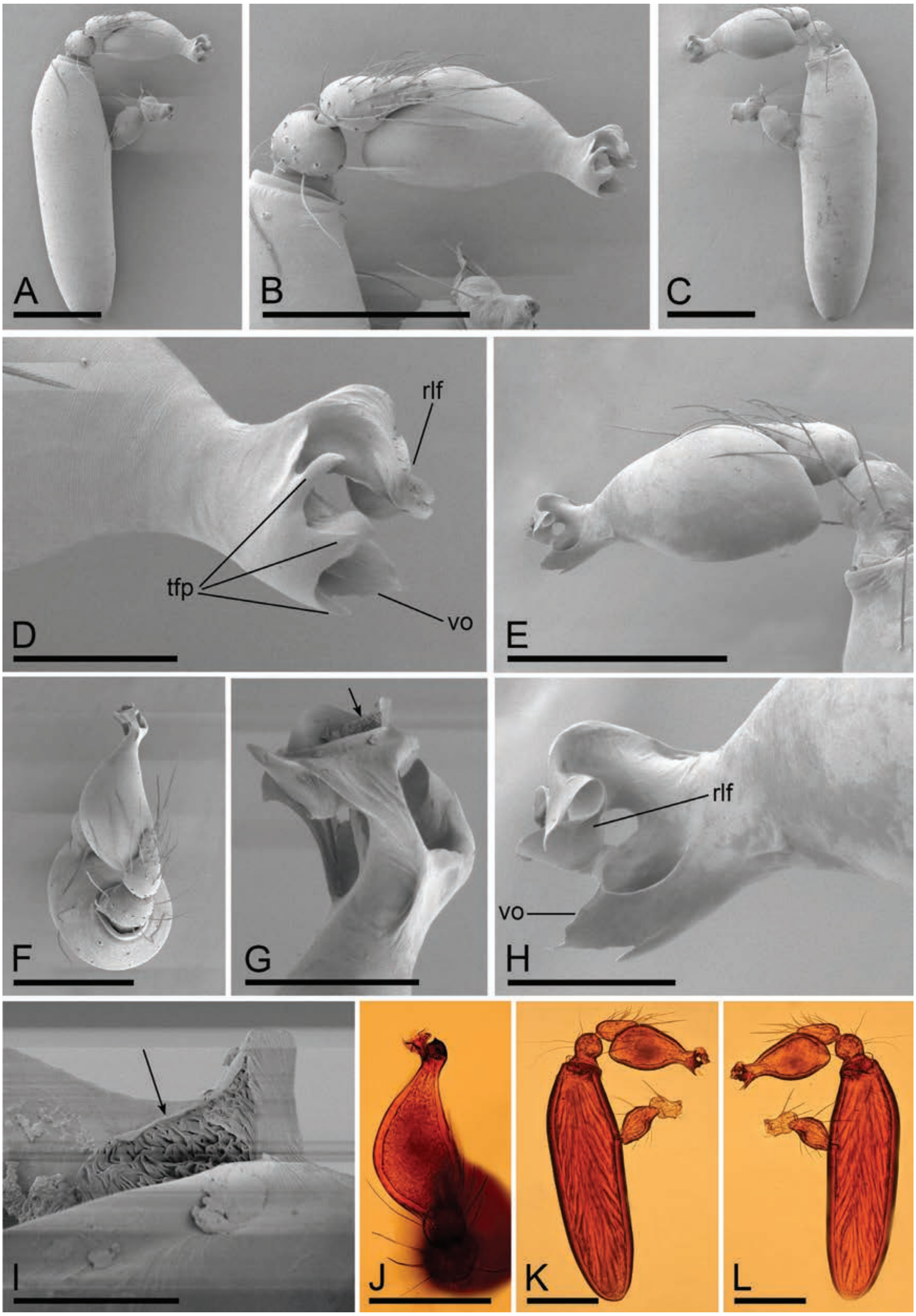


Figure 7. *Camptoscaphiella trifoliata* sp. nov., male left palp **A, K** prolateral view **B, E** bulb, prolateral and retrolateral views **C, L** retrolateral view **D, G, H** distal part of bulb, prolateral, dorsal and retrolateral views **F, J** dorsal view **I** same as **G** showing the details (arrow). Abbreviations: rlf = retrolateral fold; tfp = trifurcate process; vo = ventral outgrowth. Scale bars: 0.2 mm (**A–C, E, F, J–L**); 0.05 mm (**D, H, G**); 0.01 mm (**I**).

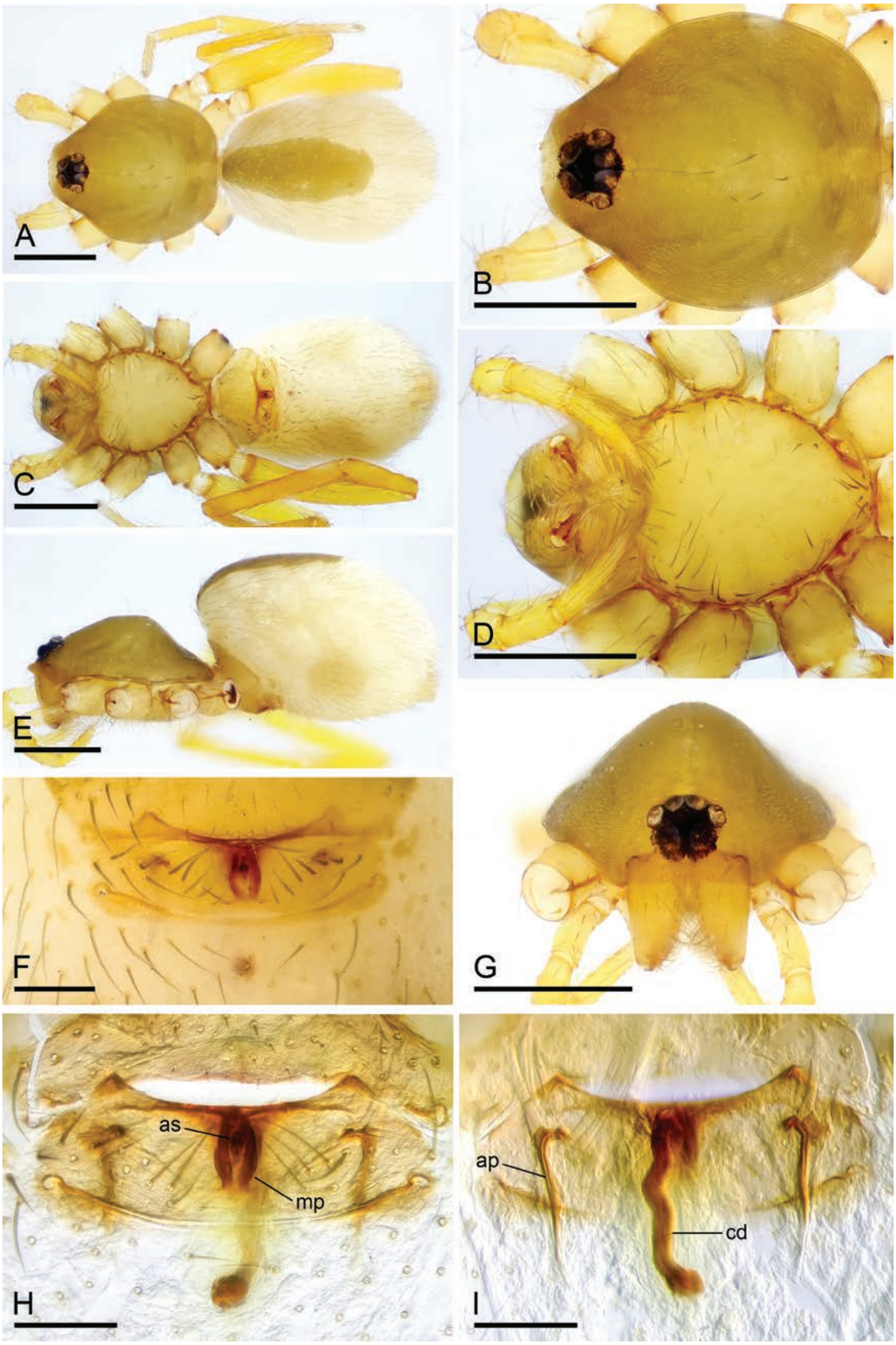


Figure 8. *Camptoscaphiella trifoliata* sp. nov., female paratype (SYNU-1146) **A, C, E** habitus, dorsal, ventral and lateral views **B, D, G** prosoma, dorsal, ventral and anterior views **F** epigastric region, ventral view **H, I** endogyne, ventral and dorsal views. Abbreviations: ap = apodemes; as = anterior sclerite; cd = copulatory duct; mp = median plate. Scale bars: 0.4 mm (**A–E, G**); 0.2 mm (**F, H, I**).

Description. Male (holotype). ***Body*:** uniformly colored, yellowish brown; habitus as in Fig. 6A, C, E; length 1.75. ***Carapace*** (Fig. 6B, F): 0.84 long, 0.68 wide; pars thoracica strongly elevated in lateral view, entire surface finely reticulated. ***Eyes*** (Fig. 6B, G): ALE: 0.07; PME: 0.05; PLE: 0.04; ALE circular, PME oval, PLE oval; posterior eye row straight from above, procurved from front; ALE separated by less than one radius. ***Clypeus*** (Fig. 6F, G): margin unmodified, straight in front view, sloping forward in lateral view. ***Mouthparts*** (Fig. 6D, G): chelicerae unmodified; anterior-median part of the endites slightly sclerotized. ***Sternum*** (Fig. 6D): as long as wide, with pointed anterolateral bumps. ***Abdomen*** (Fig. 6A, C, E): 0.91 long, 0.53 wide; oval, scuta pale orange; dorsal scutum covering about 3/4 of abdomen length, about 2/3 of abdomen width, fused to epigastric scutum; postgastric scutum small, covering about 1/2 of abdominal venter. ***Palp*** (Fig. 7A–L): reddish brown; patella extremely long club-shaped, length/width = 3.41, about 5.5 times longer than femur, and 2.5 times longer than bulb; cymbium (length/width = 1.92) narrow in dorsal view; psembolus with trifurcate process (tfp), ventral outgrowth (vo) and small retrolateral fold (rlf).

Female (SYNU-1100). As in male except for the following. ***Body*:** habitus as in Fig. 8A, C, E; length 1.94. ***Carapace*:** 0.83 long, 0.74 wide. ***Eyes*:** ALE 0.07; PME 0.05; PLE 0.06. ***Abdomen*:** 1.11 long, 0.76 wide. Postgaster (Fig. 8F, H): with rounded anterior sclerite (as) and fusiform median plate (mp). ***Endogyne*** (Fig. 8I): copulatory duct (cd) long, narrow, sinuous with tip well beyond postepigastric scutum; apodemes (ap) slender.

Etymology. The specific name, derived from Latin word *trifoliatus*, refers to the three-forked processes on the distal part of the bulb; adjective.

Distribution. Known only from the type locality.

Camptoscaphiella zayu Tong & Li, sp. nov.

https://zoobank.org/FC362C41-6FA7-450F-856B-4E16980715DD

Figs 9–11, 12

Material examined. *Holotype* China • ♂ (SYNU-1141); Xizang, Zayu Co., Chawalong Town, Long Vill.; 28°28.941'N, 98°28.193'E, 2883 m; 8.IX.2014; J. Liu leg.

***Paratypes*.** China • 1 ♀ (SYNU-1142); same data as for holotype.

Diagnosis. The new species is similar to the type species, *C. fulva* Caporiacco, 1934, but can be distinguished by the strongly sclerotized dorsal (dp) and ventral (vp) processes of the psembolus (Fig. 10G, I) vs. with two spinelike processes (Baehr and Ubick 2010: figs 161–163), and long copulatory duct (cd, Fig. 11H, I) vs. short inverted droplet-shaped copulatory duct (Baehr and Ubick 2010: figs 182, 183).

Description. Male (holotype). ***Body*:** uniformly colored, pale yellow; habitus as in Fig. 9A, C, E; length 1.91. ***Carapace*** (Fig. 9B, F): 0.85 long, 0.78 wide; pars thoracica strongly elevated in lateral view, whole surface finely reticulated. ***Eyes*** (Fig. 9B, G): ALE: 0.08; PME: 0.06; PLE: 0.06; ALE circular, PME oval, PLE oval; posterior eye row procurved from both above and front; ALE separated by less than one radius. ***Clypeus*** (Fig. 9F, G): margin unmodified, straight in front view, sloping forward in lateral view. ***Mouthparts*** (Fig. 9D, G): chelicerae unmodified; anterior-median part of the endites slightly sclerotized. ***Sternum*** (Fig. 9D): as long as wide, with pointed anterolateral bumps.

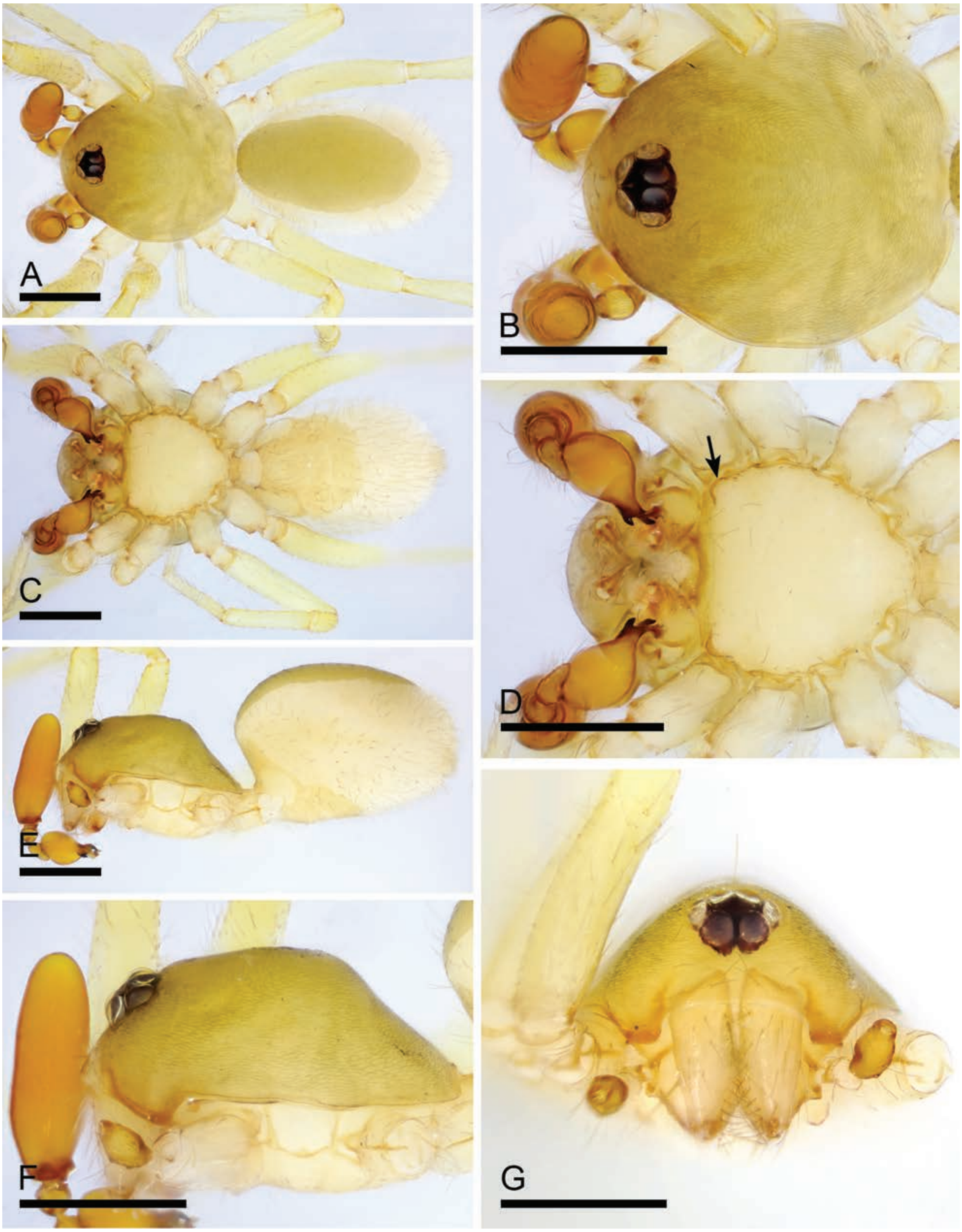


Figure 9. *Camptoscaphiella zayu* sp. nov., male holotype **A, C, E** habitus, dorsal, ventral and lateral views **B, D, F, G** prosoma, dorsal, ventral, lateral and anterior views, arrow shows the pointed anterolateral bumps. Scale bars: 0.4 mm (**A–G**).

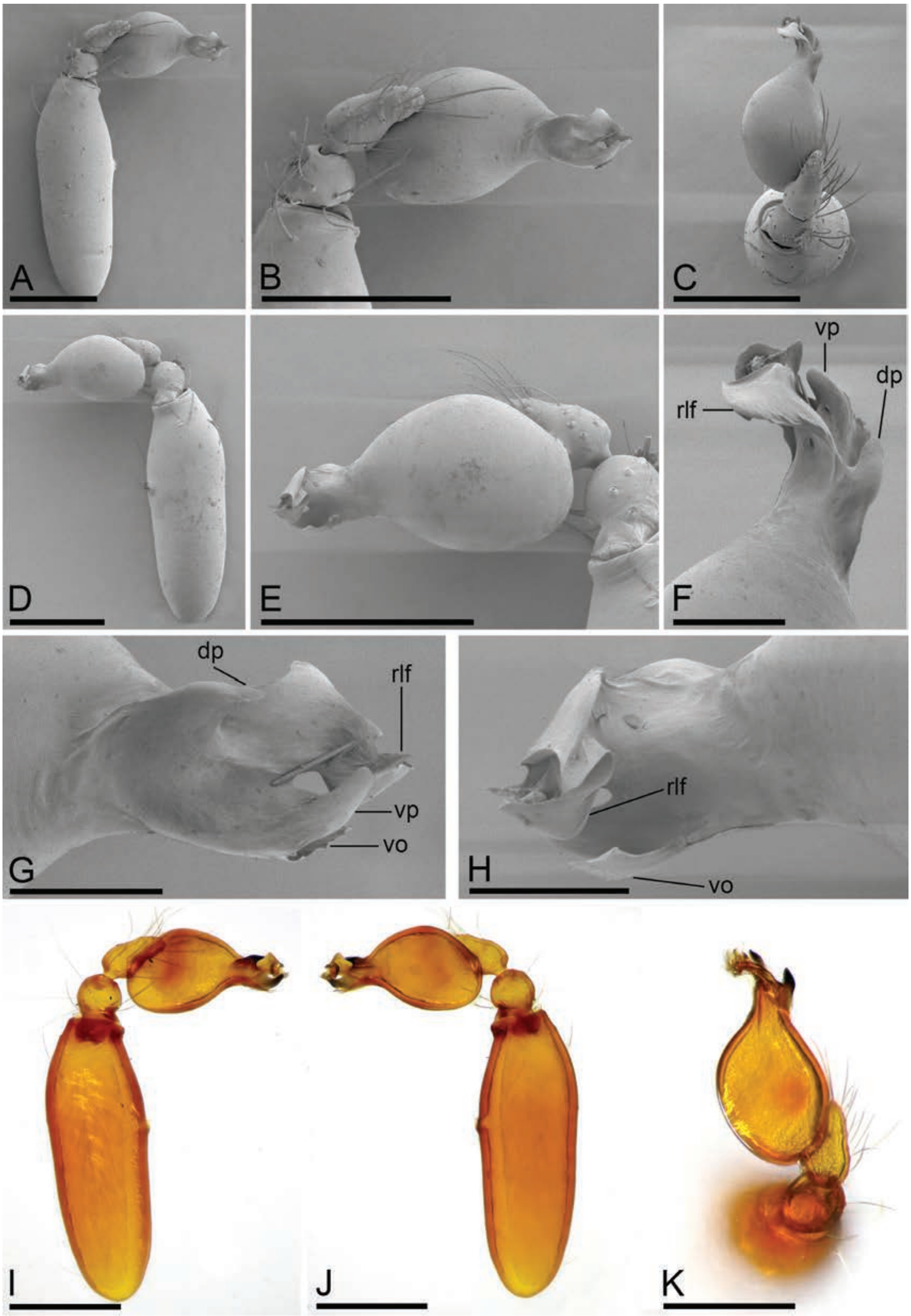


Figure 10. *Camptoscaphiella zayu* sp. nov., male left palp **A, I** prolateral view **B, E** bulb, prolateral and retrolateral views **C, K** dorsal view **D, J** retrolateral view **F, G, H** distal part of bulb, dorsal, prolateral and retrolateral views. Abbreviations: dp = dorsal process; rlf = retrolateral fold; vo = ventral outgrowth; vp = ventral process. Scale bars: 0.2 mm (**A–E, I–K**); 0.05 mm (**F–H**).

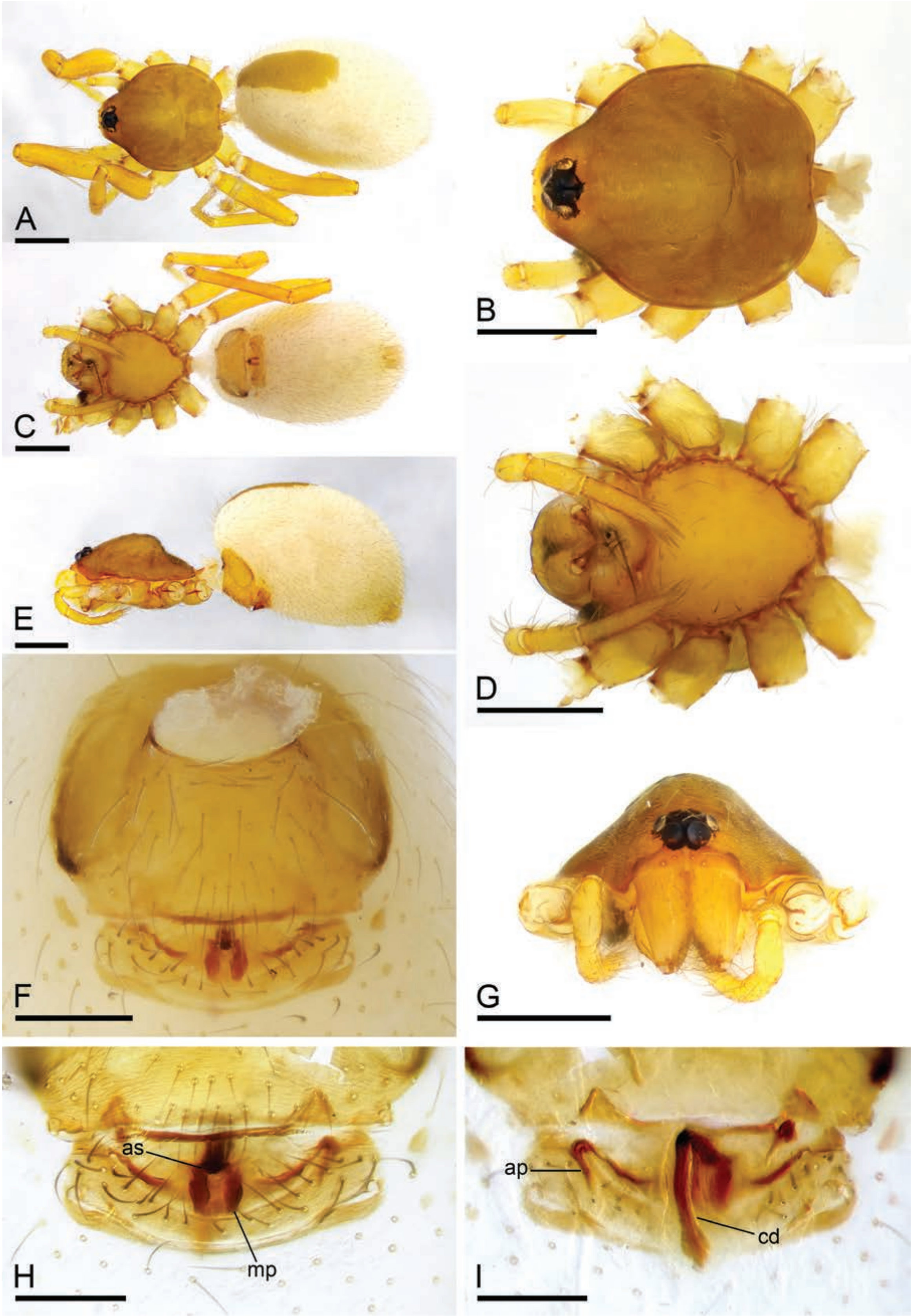


Figure 11. *Camptoscaphiella zayu* sp. nov., female paratype (SYNU-1142) **A, C, E** habitus, dorsal, ventral and lateral views **B, D, G** prosoma, dorsal, ventral and anterior views **F** epigastric region, ventral view **H, I** endogyne, ventral and dorsal views. Abbreviations: ap = apodemes; as = anterior sclerite; cd = copulatory duct; mp = median plate. Scale bars: 0.4 mm (**A–E, G**); 0.2 mm (**F, H, I**).

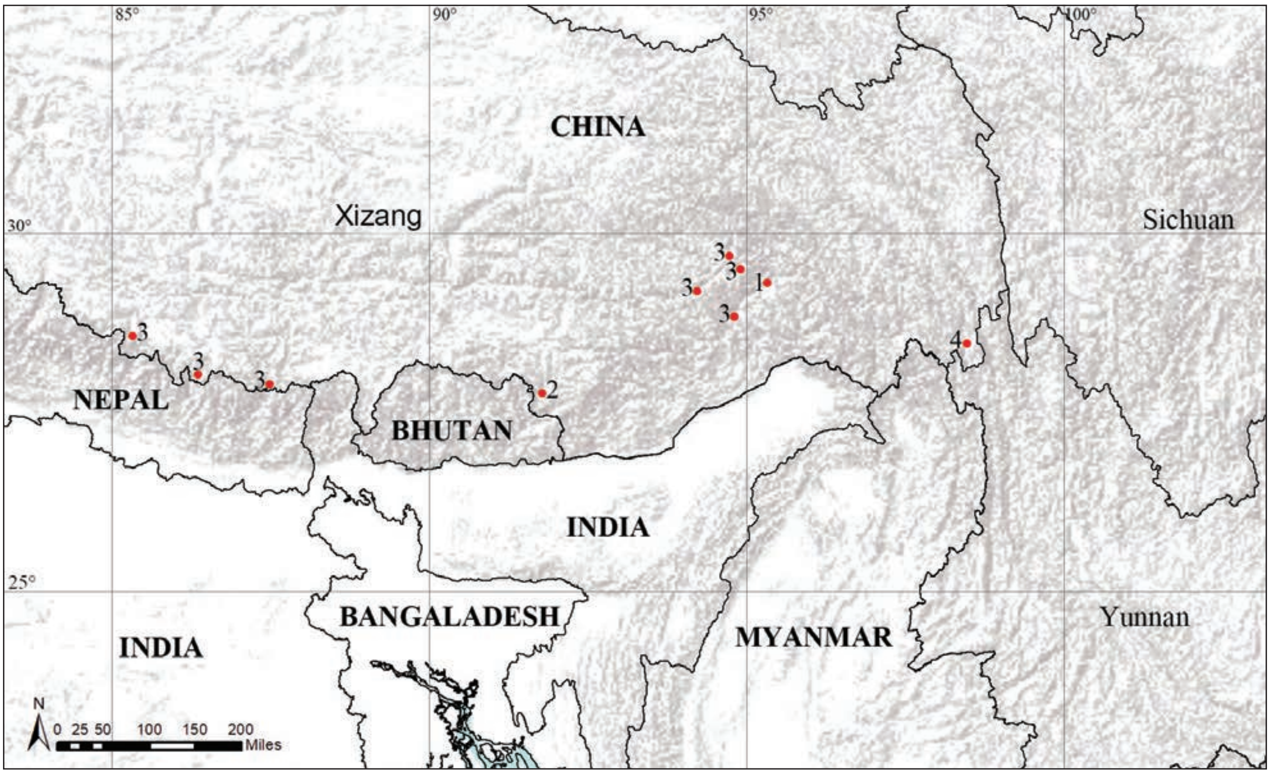


Figure 12. Distribution records of four new species of the genus *Camptoscaphiella* from Xizang, China. 1. *C. metok* sp. nov. 2. *C. shannan* sp. nov. 3. *C. trifoliata* sp. nov. 4. *C. zayu* sp. nov.

Abdomen (Fig. 9A, C, E): 1.06 long, 0.68 wide; oval, scuta pale orange; dorsal scutum covering about 5/6 of abdomen length, about 3/4 of abdomen width, fused to epigastric scutum; postgastric scutum small, covering about 1/2 of abdominal venter. ***Palp*** (Fig. 10A–K): reddish brown; patella extremely long club-shaped, length/width = 2.96, about 4.2 times longer than femur, and 2.5 times longer than bulb; cymbium narrow (length/width = 1.64) in dorsal view; psembolus with strongly sclerotized dorsal process (dp), strongly sclerotized ventral process (vp), broad ventral outgrowth (vo) and a small retrolateral fold (rlf).

Female (SYNU-1142). As in male except for the following. ***Body*:** habitus as in Fig. 11A, C, E; length 2.37. ***Carapace*:** 0.92 long, 0.81 wide. ***Eyes*:** ALE 0.07; PME 0.05; PLE 0.05. ***Abdomen*:** 1.45 long, 0.90 wide. ***Postgaster*** (Fig. 11F, H): with rounded anterior sclerite (as) and pear-shaped median plate (mp). ***Endogyne*** (Fig. 11I): copulatory duct (cd) long, narrow, straight with tip reaching groove between posterior spiracles; apodemes (ap) short.

Etymology. The specific name refers to the type locality and is a noun in apposition.

Distribution. Known only from the type locality.

Acknowledgements

Thanks to Qi Cao, Zhizhong Gao, Yejie Lin, Jincheng Liu, and Jianglang Wu for collecting specimens. The manuscript benefitted greatly from comments by Yuri M. Marusik (Magadan, Russia) and Zhisheng Zhang (Chongqing, China). Joseph K. H. Koh (Singapore) kindly checked the English of the final draft.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This study was supported by the National Natural Science Foundation of China (NSFC32370479, 31972867).

Author contributions

YT designed the study. YT and XW finished the descriptions and took the photos. YT and SL drafted and revised the manuscript.

Author ORCIDs

Xiaohan Wang https://orcid.org/0009-0000-4614-9562
Yanfeng Tong https://orcid.org/0000-0002-4348-7029
Shuqiang Li https://orcid.org/0000-0002-3290-5416

Data availability

All of the data that support the findings of this study are available in the main text.

References

Baehr BC, Harvey MS (2013) The first goblin spiders of the genus *Camptoscaphiella* (Araneae: Oonopidae) from New Caledonia. Australian Journal of Entomology 52(2): 144–150. https://doi.org/10.1111/aen.12010

Baehr BC, Ubick D (2010) A review of the Asian goblin spider genus *Camptoscaphiella* (Araneae: Oonopidae). American Museum Novitates 3697: 1–65. https://doi.org/10.1206/3697.2

Cheng W, Bian D, Tong Y, Li S (2021) A new genus and two new species of oonopid spiders from Tibet, China (Araneae, Oonopidae). ZooKeys 1052: 55–69. https://doi.org/10.3897/zookeys.1052.66402

Huang Y, Bian D, Tong Y, Li S (2021) Two new species of the genus *Camptoscaphiella* from Yunnan, China (Araneae: Oonopidae). ZooKeys 1052: 43–53. https://doi.org/10.3897/zookeys.1052.66743

Tong Y, Li S (2007) One new genus and four new species of oonopid spiders from southwest China (Araneae: Oonopidae). Annales Zoologici (Warszawa) 57: 331–340.

Tong Y, Bian D, Li S (2023) Three new species of the genus *Ischnothyreus* Simon, 1893 and the discovery of the male of *I. linzhiensis* Hu, 2001 from Tibet, China (Araneae, Oonopidae). ZooKeys 1152: 119–131. https://doi.org/10.3897/zookeys.1152.100341

Wang X, Wang Z, Tong Y, Bian D, Yang Z (2023) Three new species of *Camptoscaphiella* Caporiacco, 1934 (Araneae, Oonopidae) from Yunnan Province, China. Biodiversity Data Journal 11: e109679. https://doi.org/10.3897/BDJ.11.e109679

WSC (2024) World Spider Catalog. Version 25.0. Natural History Museum Bern. http://wsc.nmbe.ch [Accessed on: 30 April 2024]

ZooKeys 1208: 99–132 (2024)
DOI: 10.3897/zookeys.1208.119147

Research Article

Five alien achatinid land snails (Gastropoda, Eupulmonata) first reported in greenhouses of Italian botanical gardens

Giuseppe Manganelli[1,2], Andrea Benocci[3], Debora Barbato[1,2], Folco Giusti[1]

1 *Dipartimento di Scienze Fisiche, della Terra e dell'Ambiente, Università di Siena, Via Mattioli 4, 53100 Siena, Italy*
2 *NBFC (National Biodiversity Future Center), Palermo, Italy*
3 *Museo di Storia Naturale dell'Accademia dei Fisiocritici, Piazzetta S. Gigli 2, 53100 Siena, Italy*
Corresponding author: Debora Barbato (debora.barbato@unisi.it)

OPEN ACCESS

Academic editor: Eike Neubert
Received: 19 January 2024
Accepted: 4 June 2024
Published: 29 July 2024

ZooBank: https://zoobank.org/BEF04EEA-B9D0-4220-9BC4-84208488CCF2

Citation: Manganelli G, Benocci A, Barbato D, Giusti F (2024) Five alien achatinid land snails (Gastropoda, Eupulmonata) first reported in greenhouses of Italian botanical gardens. ZooKeys 1208: 99–132. https://doi.org/10.3897/zookeys.1208.119147

Abstract

Plant trade and exchange for horticulture, recreation or research play a significant role in the dispersal of molluscs. Alien slugs and snails accidentally introduced into Europe have established rich communities in several countries, but although these introductions could have ecological and economic implications, mollusc xenodiversity in Italian botanical gardens, plant nurseries, and greenhouses has never been investigated. Facilities throughout the country were therefore visited between 2017 and 2023. Here the list of the achatinoidean species so far recorded from Italian greenhouses is provided, giving a short description of their diagnostic characters. The greenhouses of Trento and Padua host interesting assemblages of achatinoideans: the results of this study include the first reports of four achatinids, namely *Allopeas clavulinum*, *Opeas hannense*, *Paropeas achatinaceum* and *Subulina octona* from Italy and the first record of *Geostilbia aperta* from Europe. Reproductive anatomy of all species except *Geostilbia aperta* is illustrated in detail, integrating anatomical knowledge of this group of tiny molluscs, some of which are known mainly from their shell characters. The systematics of all the species is discussed, highlighting topics for future research (e.g., status of *Allopeas mauritianum*, real identity of *Helix hannense*, anatomy of *Opeas hannense*, species-level taxonomy of *Subulina*, systematic relationships and species-level taxonomy of *Geostilbia*).

Key words: Geographical distribution, non-indigenous molluscs, shell and genital morphology, taxonomy, translocated species

Introduction

An increasing number of organisms of limited mobility are rapidly spreading outside their native range and habitat (Bergey et al. 2014; Pergl et al. 2017; Hulme 2021) due to the global expansion of trade and transport of goods (Hulme 2009; Seebens et al. 2017). This may have dramatic implications for local biodiversity, food crops, human health, ecosystem processes and habitat degradation (Kenis et al. 2009; Keller et al. 2011). In temperate countries, a major component of xenodiversity consists of tropical species unwittingly introduced with plants and substrates for horticulture or recreation. Botanical gardens and hothouses play a major role in the accidental introduction of foreign species (e.g., Teodorescu and Matei 2010; Heywood 2011; Szczepkowski et al. 2014; Hulme 2015; Kolicka et al. 2015; Wang et al. 2015; Jaskuła et al. 2019).

Alien slugs and snails have already established rich communities in European plant nurseries, greenhouses, and botanical gardens (e.g., Da Sois 2015; Reischütz et al. 2018; Kwitt et al. 2019) and new species arrive every year (e.g., von Proschwitz 2004; Preece and Naggs 2014; Jaskuła et al. 2019; Richling and von Proschwitz 2021). Land molluscs are easily transported with living plants via eggs in root balls or hatched individuals on leaves, stems, moss on pots, decaying plant matter on the soil surface or in the substrate (Robinson 1999; Bergey et al. 2014). However, despite the important ecological and economic implications of the introduction of alien gastropods, the non-native mollusc communities of Italian botanical gardens have not been thoroughly investigated. Therefore, our research group tried to fill this gap, visiting facilities throughout the country: here we report the rich assemblage of achatinoideans found in the first years of this study, including the first European record of *Geostilbia aperta* (Swainson, 1840).

Achatinoideans include several travelling snails (e.g., species that have the ecological flexibility to survive long journeys and spread and prosper in their new habitats; Smith 1989) that have been unintentionally introduced outside their native range through plant trade and exchanges: some have now achieved a pantropical distribution, while others, widespread in greenhouses and plant nurseries, have become cosmopolitan and occur in very high densities in such anthropogenic habitats. So far seven species have been recorded from European greenhouses and hothouses: *Allopeas clavulinum* (Potiez & Michaud, 1838), *Allopeas gracile* (Hutton, 1834), *Leptinaria unilamellata* (d'Orbigny, 1838), *Opeas hannense* (Rang, 1831), *Paropeas achatinaceum* (Pfeiffer, 1846), *Subulina octona* (Bruguière, 1789), *Subulina striatella* (Rang, 1831) (Horsák et al. 2020).

As pointed out by Horsák et al. (2020) and Richling and von Proschwitz (2021), it is not easy to distinguish these small similar-looking snails, especially for scientists in countries where such genera and species are not native. Tiny achatinoideans include many described taxa, the great majority of which live in tropical areas relatively neglected by research biologists. The taxonomy of this speciose group is still being defined and shell-based identifications are not considered very reliable (Solem 1989; Naggs 1994; von Proschwitz 1994; Cowie 1997; Thompson 2011; Brodie and Barker 2012; Gittenberger and van Bruggen 2013; Budha et al. 2015; Horsák et al. 2020; Richling and von Proschwitz 2021). There is evidence that a conchological approach has often caused generic misallocations and species misidentifications (Cowie 1997, 2000; Gittenberger and van Bruggen 2013; Budha et al. 2015).

Anatomical dissection of small achatinoideans is not easy: the proximal part of the penial complex is difficult to interpret since its components are so reduced and closely packed as to appear a single structure. Nor are anatomical differences between extant genera very evident. Nevertheless, although anatomical study may only provide partial solutions, it is absolutely necessary because generic taxa were defined on anatomical characters so that identification is only possible by this examination. The aim of the paper is to list the species of achatinoideans so far recorded from Italy, giving a short description of their diagnostic shell and anatomical characters in order to facilitate identification, and understanding of their taxonomic and nomenclatural framework.

Materials and methods

Between 2017 and 2023, the tropical greenhouses of seven facilities in central and northern Italy (Science Museum of Trento (MUSE); botanical gardens of Siena, Florence, Pisa, Padua, Bologna, and Milan) were visited and inspected for alien molluscs as part of the XenoDOMuS project on xenodiversity in tropical greenhouses of Italian botanical gardens and scientific museums.

Snails and slugs were detected by visual search and by collecting leaf litter and surface soil. The visual search enabled detection of larger specimens, while collection of litter and soil revealed smaller species. The litter and soil were dried and sieved through decreasing mesh sizes. The coarser fraction was sorted visually, the others under a stereomicroscope. Although this method involves a huge investment in terms of sampling effort and time, it ensures more efficient collection of small mollusc species than a visual search.

Identifications were based on morphological features (i.e., shell and anatomical characters). Live specimens were drowned in water, then fixed and preserved in 75% ethanol buffered with sodium carbonate. The bodies were dissected under a light microscope using fine-pointed watchmaker's forceps. Anatomical organs were drawn using a camera lucida. Anatomical nomenclature usually followed the standard references for Eupulmonata (e.g., Manganelli et al. 2022 and references therein); as regards the proximal penial complex, the terms epiphallus and penial caecum are in customary use in the "subulinids" (e.g., Naggs 1994; Gittenberger and van Bruggen 2013).

The descriptive terms (e.g., short vs long, slender vs wide) refer to comparisons of the same section of the genitalia in different taxa of achatinids. The directional terms proximal, basal, and initial denote the part closer to the gonad, whereas distal, apical, final, and terminal denote the part closer to the gonopore in the case of ducts of the main axis of the genitalia (e.g., free oviduct, vagina, vas deferens, penis). The same terms denote the part closer to (proximal, basal, or initial) or further from (distal, apical, final, or terminal) the main axis of the genitalia in the case of blind structures radiating from the main axis of the genitalia (bursa copulatrix, penial/vaginal/atrial appendix, etc.).

The material is stored in the G. Manganelli collection (GMC; Dipartimento di Scienze Fisiche, della Terra e dell'Ambiente, Università di Siena, Italy).

Acronyms of the shell variables:

AH	aperture height,	**SD**	shell diameter,
AW	aperture width,	**SH**	shell height.

Acronyms of the anatomical organs:

AG	albumen gland,
BC	bursa copulatrix (gametolytic gland),
BW	body wall,
DBC	duct of bursa copulatrix,
DP	distal penis,
DV	distal vagina,
Eg	egg/eggs in the uterine spermoviduct,
Ep	epiphallus,

FHD	first hermaphrodite duct,
FO	free oviduct,
GA	genital atrium,
LB	vaginal lateral bulge,
P	penis,
PC	penial caecum,
PP	proximal penis,
PR	penial retractor,
PS	penial sheath,
PSO	prostatic spermoviduct,
SOD	spermoviduct (ovispermiduct; second hermaphrodite duct),
USO	uterine spermoviduct,
V	vagina,
VD	vas deferens.

Results

Non-native molluscs were observed in all the facilities investigated, but achatinids were only found in Padua (3 species: *Allopeas clavulinum*, *Paropeas achatinaceum*, *Subulina octona*) and Trento (4 species: *Allopeas clavulinum*, *Opeas hannense*, *Subulina octona*, *Geostilbia aperta*). In these two greenhouses, high densities of small achatinids and other exotic slugs, snails, and soil invertebrates were found. The systematics, morphology, ecology, and distribution of the five species of achatinids are described below. A small undescribed slug of the little-known systellommatophoran family Rathouisiidae found in the tropical greenhouse of the Science Museum of Trento (MUSE) has already been described (Manganelli et al. 2022).

Family Achatinidae Swainson, 1840

The superfamily Achatinoidea Swainson, 1840 has a complex and still unresolved systematic framework. Nordsieck (1986) included five families in this group (Achatinidae Swainson, 1840, Ferussaciidae Bourguignat, 1883, Subulinidae Fischer & Crosse, 1877, Coeliaxidae Pilsbry, 1907, and Thyrophorellidae Girard, 1895), while Bouchet and Rocroi (2005) listed only four (Achatinidae, Ferussaciidae, Subulinidae, Micractaeonidae Schileyko, 1999). On the other hand, Schileyko (1999) only included the Achatinidae in the Achatinoidea, and grouped Subulinidae, Glessulidae Godwin-Austen, 1920, Micractaeonidae, and Ferussaciidae in their own superfamily, Subulinoidea Fischer & Crosse, 1877. Fontanilla et al. (2017) published a multi-gene phylogenetic analysis of the achatinoideans examining 24 taxa from five achatinoid families (Achatinidae, Coeliaxidae, Ferussaciidae, Subulinidae, and Thyrophorellidae). The results suggest that the family level systematics requires a radical re-evaluation because among the traditionally recognised families, only Achatinidae are monophyletic whereas Ferussaciidae, Coeliaxidae, and Subulinidae are polyphyletic or unresolved and members of the Coeliaxidae and Thyrophorellidae cluster among the subulinids.

In their “Revised classification, nomenclator and typification of gastropod and monoplacophoran families”, Bouchet et al. (2017), following Fontanilla et al. (2017), moved the Subulinidae, Coeliaxidae, Thyrophorellidae, and the ferussaciid genus *Cecilioides* Férussac, 1814 to the Achatinidae. However, in the absence of a more comprehensive molecular study of members of all the families and subfamilies previously recognised in the achatinoideans, they proposed a preliminary classification in which most of the subfamilies listed by Schileyko (1999) were treated as valid and allocated *Cecilioides* to a distinct subfamily (Cecilioidinae Mörch, 1864). It is nonetheless possible that the removal of *Cecilioides* from the Ferussaciidae was based on a misidentification of the species examined by Fontanilla et al. (2017) (E. Neubert, pers. comm. 7 May 2024). Indeed MolluscaBase (MolluscaBase eds 2024a) still lists *Cecilioides* in the family Ferussaciidae, albeit citing Bouchet et al. (2017) as the source for the page dealing with Achatinidae. Thus, in the absence of a more consistent classification at subfamily level, the species considered in the present study are simply taken in alphabetical rather than systematic order, with the exception of *Geostilbia* Crosse, 1867, traditionally considered a ferussaciid based solely on shell characters, which we consider last. The inclusion of *Geostilbia* in the ferussaciids is based on its close shell similarity with *Cecilioides*, but without anatomical and molecular evidence, its attribution to a different group/superfamily cannot be excluded.

Allopeas clavulinum (Potiez & Michaud, 1838)

Bulimus clavulinus Potiez & Michaud, 1838, 1: 136, pl. 14, figs 9, 10. Type locality: "L'île Bourbon", namely Réunion Island, Mascarene Archipelago. Type material: lost (Smith 1992: 309).

Material examined. ITALY • 6 shells and 6 spirit specimens; Trento, Tropical greenhouse of the Science Museum of Trento (MUSE); 46°03'45.16"N, 11°06'50.08"E; 14 Dec. 2017; A. Benocci, G. Manganelli, D. Miserocchi leg.; GMC 47556 • 623 shells, 10 spirit specimens; same locality; 04 Jan. 2019, 10 Feb. 2019, 04 May 2019; D. Barbato, G. Bolzonella leg.; GMC 51194 • 418 shells, 2 spirit specimens; same locality; 01 Feb. 2022; D. Barbato, A. Benocci leg.; GMC 51184 • 133 shells; same locality; 02 Feb. 2023; F. Rossi leg.; GMC 57343 • 155 shells; same locality; 9 Feb. 2023; D. Barbato, A. Benocci leg.; GMC 57350 • 145 shells and 1 spirit specimen; Padua, Biodiversity Garden (Botanical Garden of Padua); 45°23'52.59"N, 11°52'50.37"E; 06 Mar. 2019; D. Barbato leg.; GMC 57373.

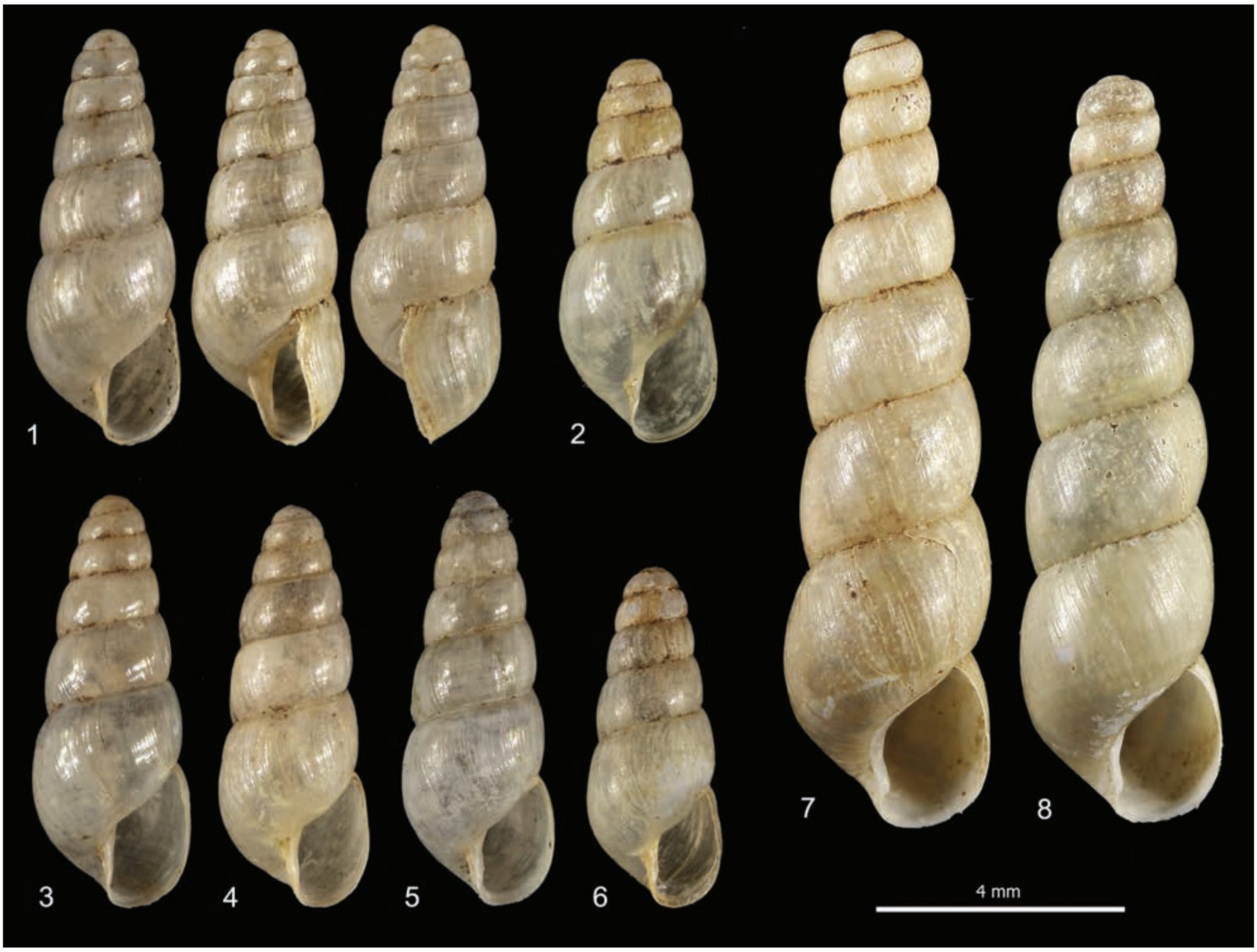
Description. ***Shell*** (Figs 1–6). Dextral, small, minutely perforate to imperforate, elongate, slender, conical, rather robust, pearly off-white, glossy and sub-transparent when fresh, with 5–7 slightly convex whorls, separated by moderately deep sutures. Apex obtuse, rounded, and smooth. Last whorl ~ 1/2 of shell height. Aperture small, ~ 1/3 of shell height, obliquely pyriform, slightly prosocline. Peristome interrupted, not thickened, only slightly reflected on columella, sometimes with slightly evident callous rim on parietum; columella straight; outer margin sinuous in lateral view (approximately inverse S-shaped). Protoconch smooth; teleoconch with thin and irregular collabral growth lines. Shell dimensions: SH 5.5–6.8 mm; SD 2.2–2.6 mm; AH 1.9–2.3 mm; AW 1.2–1.4 mm.

Female distal genitalia (Figs 9–12). Free oviduct long and wide. Bursa copulatrix sac-like, oval with long slender duct (slightly longer than bursa copulatrix), sometimes initially flared. Vagina short and wide (approximately as long as free oviduct) with small lateral bulge.

Male distal genitalia (Figs 9–13, 15, 16). Vas deferens almost uniform in diameter (very thin to thin along its entire length), entering penial complex at its proximal end. Penial complex consisting of epiphallus, penial caecum and penis. Epiphallus very short. Penial caecum very short (as long as epiphallus). Penis short to rather long, almost uniformly cylindrical, undivided, with penial sheath enveloping its distal tract. Penial retractor muscle bifid, one branch inserted on proximal end of epiphallus, one branch on tip of penial caecum.

Genital atrium (Figs 9–12). Rather long.

Remarks. Although *Allopeas clavulinum* is a well-known greenhouse snail (Kerney and Cameron 1979), its taxonomic and systematic placement is still not definitive, nor is its native range clear. The species was first described from Réunion Island (as Île Bourbon), Mascarene archipelago, in the western Indian Ocean (Potiez and Michaud 1838), but Griffiths and Florens (2006) thought it an East African species introduced into the Mascarene islands. The hypothesis that the species is native to Africa or East Africa was also maintained by Kerney and Cameron (1979), Robinson (1999), Probst (2001), Shea (2007), Cowie et al. (2008), Stanisic et al. (2010), and Foon et al. (2017). However Rowson et al. (2010) observed that Verdcourt, familiar with *A. clavulinum* in botanic gardens of the UK, never reported it from East Africa (e.g., Verdcourt 1983, 2000, 2006).



Figures 1–8. Shells of alien achatinids in Italian greenhouses: **1–6** shells of *Allopeas clavulinum* from the tropical greenhouse of the Science Museum of Trento (MUSE), D. Barbato & G. Bolzonella leg. 04 May 2019 **7, 8** shells of *Subulina octona* from the tropical greenhouse of the Science Museum of Trento (MUSE), D. Barbato & G. Bolzonella leg. 04 May 2019.

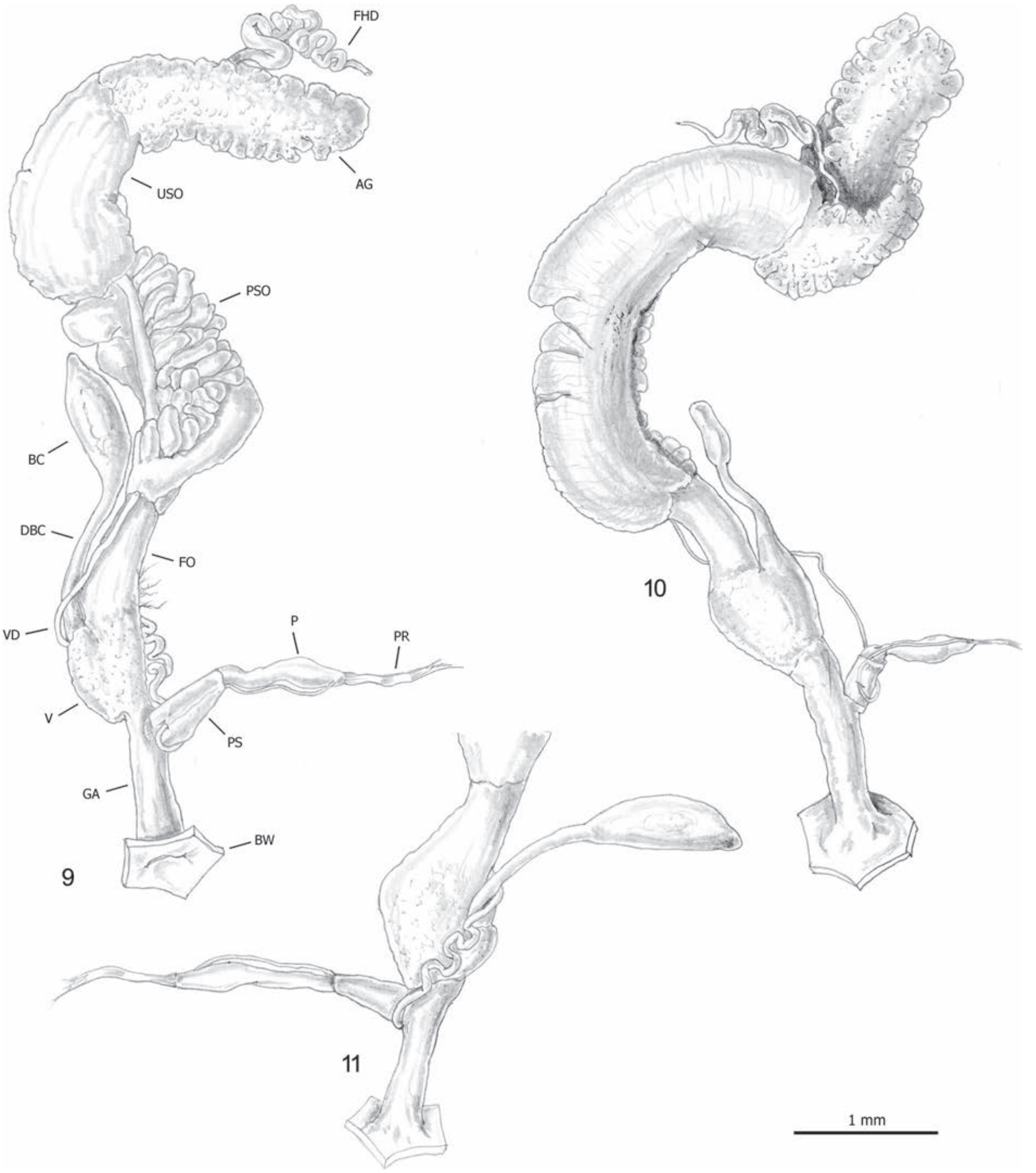
Alternatively an Asian / south-east Asian origin was proposed by Brook et al. (2010) and Rumi et al. (2010). Support for a south-east Asian origin could come from the putative finding of a shell in the Holocene of Thailand (Robba et al. 2007) and its membership of a molecularly based monophyletic group, including other species from Sri Lanka (Fontanilla et al. 2017).

Today, *Allopeas clavulinum* occurs in humid tropical and subtropical lowlands across the world. It is reported from the West Indies, South America, West Indian Ocean islands, South and South-east Asia, New Guinea, Australia, and Pacific islands. Outside the tropics and subtropics it only occurs in heated greenhouses or very disturbed habitats, mainly in the northern hemisphere. Indeed it has been reported from North America, Europe, the Middle East, and New Zealand (see Table 1 for details and references). An alleged distinct subspecies *Allopeas clavulinum kyotoense* (Pilsbry & Hirase, 1904) is reported from Korea and Japan (Minato 1988; Noseworthy et al. 2007).

The genital anatomy of *Allopeas* species is poorly understood. Earlier studies have been performed on specimens of *Allopeas gracile* (Hutton, 1834) from Puerto Rico (Baker 1945; Baker in Pilsbry 1946) and Suriname (Gittenberger and van Bruggen 2013), *Allopeas clavulinum* from Scotland (Baker 1945; Baker in Pilsbry 1946) and Brazil (Marcus and Marcus 1968), *Allopeas mauritianum* (Pfeiffer, 1853) from Mauritius (Baker 1945; Baker in Pilsbry 1946) and *Allopeas* “spec. 2 and *Allopeas* spec. 3” from Pemba (Gittenberger and van Bruggen 2013). The overall distal genitalia organisation of our specimens (Figs 9–12) is consistent with that described in *Allopeas gracile* (Baker 1945: 88–89; Baker in Pilsbry 1946: 178, fig. 84.9; Gittenberger and van Bruggen 2013: 255, fig. 10), *Allopeas clavulinum* (Baker in Pilsbry 1946: fig. 84.6; Marcus and Marcus 1968: fig. 9), *Allopeas* spec. 2 (Gittenberger and van Bruggen 2013: 254–255, fig. 11) and *Allopeas* spec. 3 (Gittenberger and van Bruggen 2013: 255, fig. 12). However the relationships between the penial sheath and the vas deferens seem different from what was illustrated by Marcus and Marcus (1968), the only authors to describe them: according to Marcus and Marcus (1968: fig. 9) the

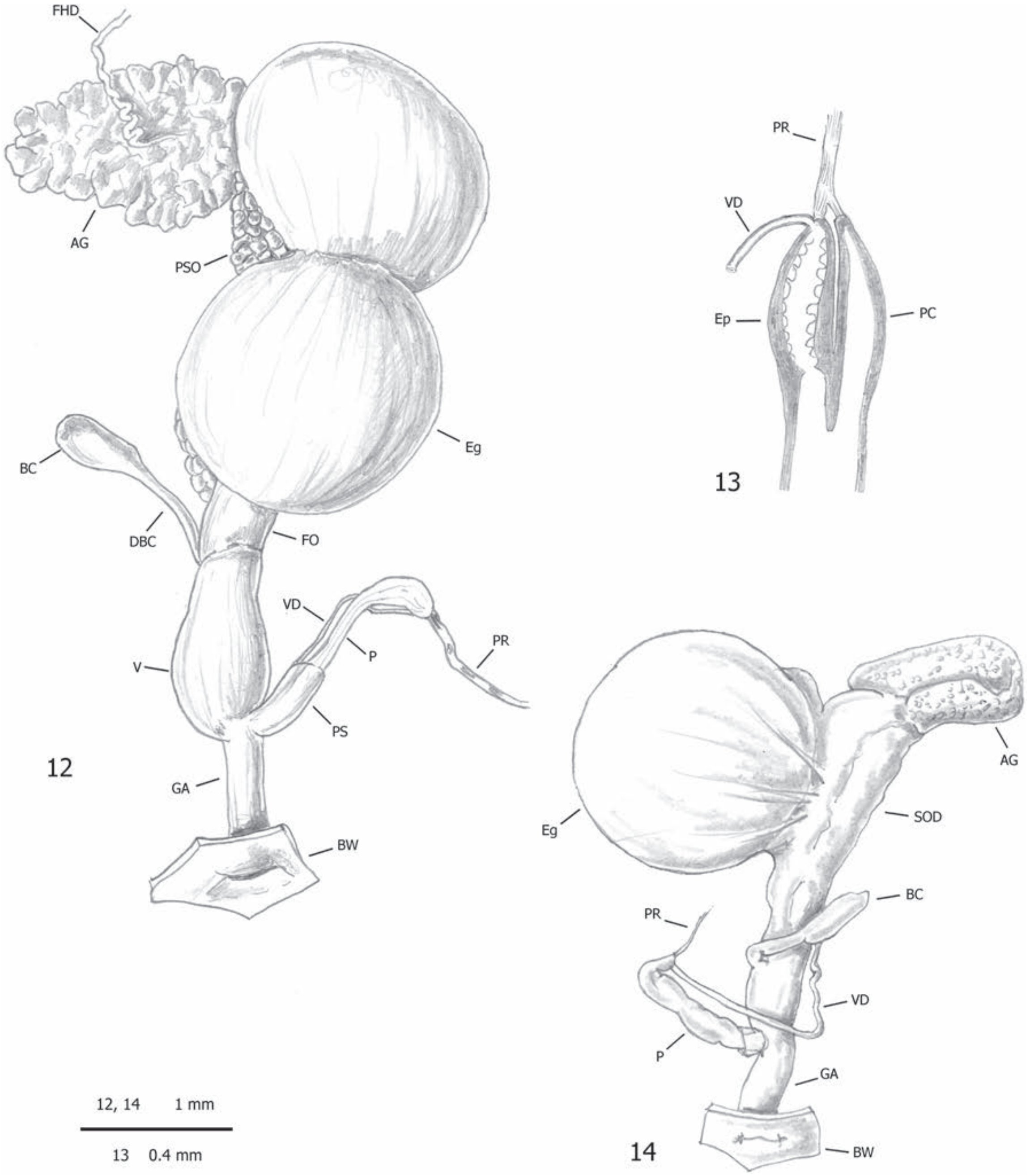
Table 1. Geographical distribution of *Allopeas clavulinum*. Asterisks indicate countries / islands where the species has been recorded only in greenhouses or very disturbed anthropogenic habitats.

Regions	Countries / Islands	References
North America	United States*	Dundee (1974), Nekola (2014)
West Indies	Hispaniola	Espinosa and Robinson (2021)
South America	Brazil and Suriname	Marcus and Marcus (1968), van Regteren Altena (1975), Simone (2006), Rumi et al. (2010)
Europe	Austria*, Czech Republic*, Finland*, Germany*, Great Britain*, Ireland*, Italy*, Netherlands* and Sweden*	Kerney and Cameron (1979), von Proschwitz (1994), Leiss and Reischütz (1996), Horsák et al. (2004, 2020), Da Sois (2015), Reischütz et al. (2018), Anderson and Rowson (2020), this paper
Indian Ocean	Madagascar, Mascarene, and Seychelles	Probst (2001), Gerlach (2006), Griffiths and Florens (2006), Bank and Menkhorst (2008), Emberton et al. (2010)
West Asia	Israel*	Mienis et al. (2012)
South Asia	Nepal	Budha et al. (2015)
South-East Asia	Indonesia, Peninsular Malaysia, Philippines, Sabah in Malaysian Borneo and Singapore	Ho (1995), Foon et al. (2017), Phung et al. (2017), Nurinsiyaha and Hausdorf (2019), Parcon et al. (2020)
Oceania	Australia, New Guinea, New Zealand* and Pacific islands (American Samoa, Chilean Islands: Rapa Nui, Cook Islands, Fiji, French Polynesia, Hawaii, Norfolk Island, Pitcairn Islands and Tonga)	Anonymous undated, van Benthem Jutting (1964), Solem (1989), Cowie (2000, 2001), Shea (2007), Stanisic et al. (2007, 2010), Brook et al. (2010), Brook (2014), Cowie et al. (2017), Maynard et al. (2018), Osorio (2018)



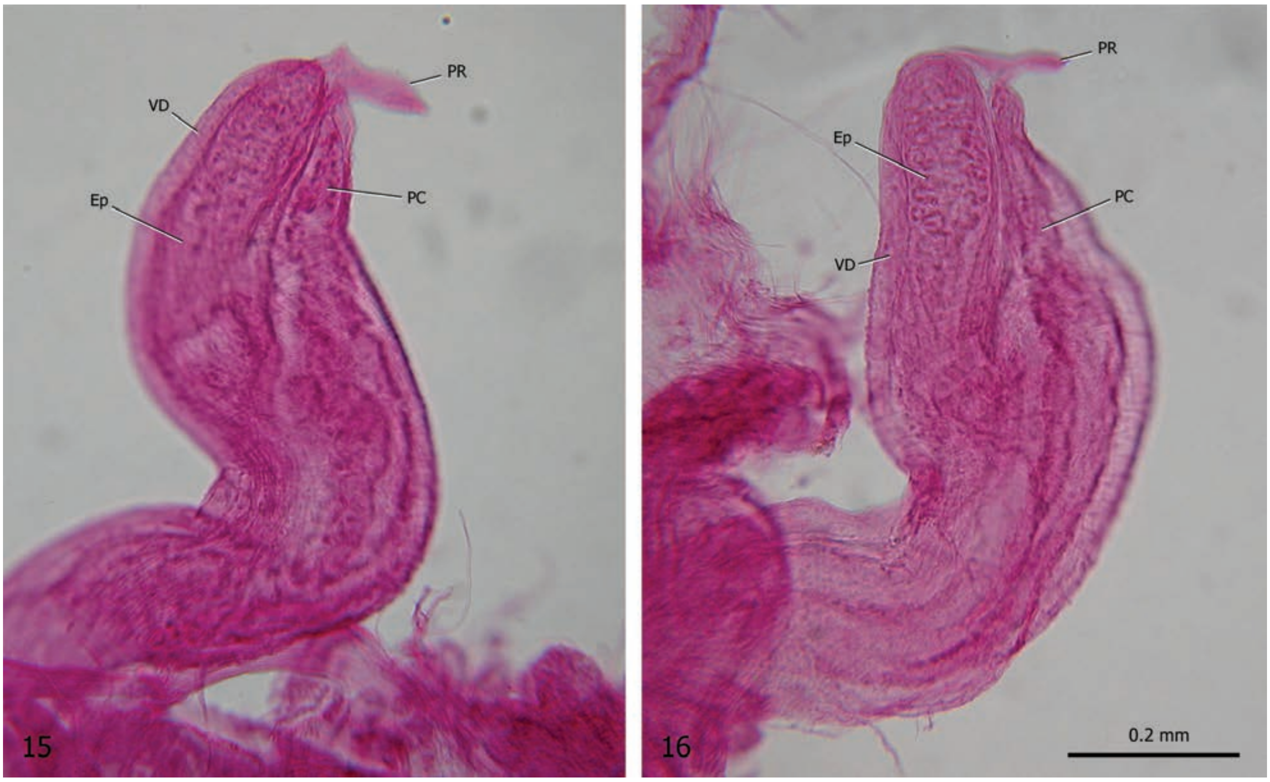
Figures 9–11. Genital anatomy of *Allopeas clavulinum* from the tropical greenhouse of the Science Museum of Trento (MUSE), D. Barbato & G. Bolzonella leg. 04 May 2019: **9, 10** genitalia (hermaphrodite gonad excluded) **11** distal genitalia.

vas deferens runs externally to the penial sheath whereas we found that it runs internally. The proximal penial complex consists of a short bulbous epiphallus and thin walled penial caecum with a branch of the penial retractor on the proximal tip of each (Figs 13, 15, 16). The epiphallus and the penial caecum are so closely juxtaposed as to resemble a usual proximal penis tip with an undivided penial retractor joined to it (Figs 9–12). This arrangement matches that already described in *Allopeas gracile* (Baker 1945: 88; Baker in Pilsbry 1946: 178, fig. 84.10), *Allopeas clavulinum* (Baker 1945: 90; Baker in Pilsbry 1946: 180, fig. 84.6; Marcus and Marcus 1968: fig. 9), *Allopeas mauritianum* (Baker 1945: 90; Baker



Figures 12–14. Genital anatomy of alien achatinids in Italian greenhouses: **12, 13** genitalia (hermaphrodite gonad excluded) and diagram of the proximal penial complex of *Allopeas clavulinum* from the tropical greenhouse of the Science Museum of Trento (MUSE), D. Barbato & G. Bolzonella leg. 04 May 2019 **14** genitalia (hermaphrodite gonad excluded) of *Opeas hannense* from the tropical greenhouse of the Science Museum of Trento (MUSE), D. Barbato & G. Bolzonella leg. 04 May 2019.

in Pilsbry 1946: 180) and *Allopeas* spec. 2 (Gittenberger and van Bruggen 2013: 255, fig. 11b). However there seems to be some variation, especially in the structure of the penial caecum between these species: *Allopeas gracile* and *Allopeas mauritianum* have a robust penial caecum, large at the base and progressively tapering towards the tip (for *Allopeas gracile*, see Baker in Pilsbry 1946: fig. 84.10; Gittenberger and van Bruggen 2013; for *Allopeas mauritianum*, see Baker in Pilsbry 1946: fig. 84.3), whereas *Allopeas clavulinum* has a long slender penial caecum almost uniform in diameter, thin along its entire length (Baker in Pilsbry 1946: fig. 84.4; Marcus and Marcus 1968: fig. 9). Based on penial caecum struc-



Figures 15, 16. Proximal penial complex of *Allopeas clavulinum* from the tropical greenhouse of the Science Museum of Trento (MUSE), D. Barbato & G. Bolzonella leg. 04 May 2019.

ture, our specimens apparently do not match those assigned to *Allopeas clavulinum* but are more similar to those assigned to *Allopeas mauritianum*. As already rightly observed by Gittenberger and van Bruggen (2013), it is not clear whether these differences are due to individual variation or to phylogenetic divergence. The relationships between these taxa are also uncertain, as is whether these names have been used consistently in the literature. Although they are currently regarded as synonyms (MolluscaBase eds 2024b), their status and relationships are still not clear and may only be defined after the designation of neotypes and study of an appropriate number of populations using an integrative approach with conchological, anatomical and molecular characters. For now we consider this species according to its current concept (e.g., Horsák et al. 2020).

Allopeas clavulinum has been found in the tropical greenhouse of MUSE, where it is the commonest and most abundant achatinid species, and in the Biodiversity Garden (Botanical Garden of Padua), where it is rather uncommon. This is the first report from Italy.

Opeas hannense (Rang, 1831)

Helix hannensis Rang, 1831: 41–42, pl. 3, fig. 8. Type locality: Senegal, Cape Verde Peninsula, Hann village (“village de Hann sur la presqu’île du Cap-Verd”). Type material: unknown.

Material examined. ITALY • 47 shells and 1 spirit specimen; Trento, Tropical greenhouse of the Science Museum of Trento (MUSE); 46°03'45.16"N, 11°06'50.08"E;

4 Jan. 2019, 10 Feb. 2019, 04 May 2019; D. Barbato, G. Bolzonella leg.; GMC 51196 • 17 shells; same locality; 01 Feb. 2022; D. Barbato, A. Benocci leg.; GMC 51187 • 1 shell; same locality; 02 Feb. 2023; F. Rossi leg.; GMC 57345 • 6 shells; same locality; 09 Feb. 2023; D. Barbato, A. Benocci leg.; GMC 57352.

Description. ***Shell*** (Figs 17–20). Dextral, very small in size, very minutely perforate, elongate, very slender, conical, rather robust, pearly off-white, glossy or waxy and sub-transparent when fresh, with 5–6 slightly convex whorls separated by moderately deep sutures. Apex obtuse, rounded, and smooth. Last whorl ~ ½ of shell height and less convex than preceding ones. Aperture small, ~ 1/3 of shell height, obliquely pyriform, slightly prosocline. Peristome interrupted, not thickened, only slightly reflected on columella, sometimes with subtle callous rim on parietum; columella straight; outer margin sinuous in lateral view (approximately inverse S-shaped). Protoconch smooth; teleoconch with weak irregular collabral growth lines. Shell dimensions: SH 4.0–4.8 mm; SD 1.6–1.8 mm; AH 1.6–1.7 mm; AW 0.9–1.0 mm.

Female distal genitalia (Fig. 14). Free oviduct very short and wide. Bursa copulatrix sac-like, oval with short slender duct (as long as bursa copulatrix), initially not flared. Vagina very short and wide (as long as free oviduct).

Male distal genitalia (Fig. 14). Vas deferens almost uniform in diameter (very thin to thin along its entire length), entering penial complex at its proximal end. Penial complex apparently consisting only of penis. Penis short, almost uniformly cylindrical with thin short penial sheath enveloping its distal tract. Penial retractor muscle inserted on proximal end of penis.

Genital atrium (Fig. 14). Rather long.

Remarks. The species was first named *Helix clavulus* by Férussac (1821: 52) based on specimens from Guadeloupe and then *Helix goodalli* by Miller (1822: 381) on specimens from near Bristol, England. Unfortunately Férussac's name was not accompanied by a description, a definition, or an indication and

Figures 17–20. Shells of *Opeas hannense* from the tropical greenhouse of the Science Museum of Trento (MUSE), D. Barbato & G. Bolzonella leg. 04 May 2019. Shell material of this species belonged mainly to juveniles; the shells depicted in the figures were the best available, although some are from specimens that were not fully grown.

so it is not available, whereas Miller's name, extensively used until the early 20th century (cf. Pilsbry 1906b), turned out to be a junior homonym and was replaced by *Bulimus pumilus* established by Pfeiffer (1840) on specimens from Cuba (cf. Pilsbry 1910). Pilsbry (1906a: 141–142) also discussed the hypothesis of Wollaston (1878: 510) that *Helix goodalli* was a junior synonym of *Helix hannense* established by Rang (1831) on specimens from the Cape Verde Peninsula, Senegal, observing: "whether this course was well-founded is a question which must remain unsettled until specimens from Rang's original locality can be compared." Consequently he never adopted Rang's name for this species (cf. Pilsbry 1946: 181–182). The synonymy of the two species was reproposed by Groh (1983) based on study of the original descriptions and the literature, and has subsequently been adopted by most recent authors (e.g., von Proschwitz 1994; Cowie 1997, 2000; Chase and Robinson 2001; Bank and Menkhorst 2008; Gerber and Clark 2015; Horsák et al. 2020). Perplexity persists about the real identity of the species described by Rang. Only the dimensions, which are consistent with those of an *Opeas* species, support Groh's interpretation. Otherwise the situation remains as described by Pilsbry more than a hundred years ago: type material of Rang's species is unknown; no one has reported or studied material from the type locality, which when Rang visited it, was a small village, today englobed in the city of Dakar (where a green area, the Parc forestier et zoologique de Hann, still survives in Hann); finally Rang's description and illustration are completely inadequate to establish the identity of the species he treated; his figure depicts a snail with shell having all the whorls quite round, whereas this species has the last whorl almost flat (incidentally Robinson (1999: table 1) considered *Opeas hannense* to be absent from Africa).

Opeas hannense is regarded as native to tropical America (Pilsbry 1946; Kerney and Cameron 1979; Deisler and Abbott 1984; Cowie 1997; Cowie et al. 2008; Brook et al. 2010; Miquel and Herrera 2014) where it is widespread in Central America and the West Indies. On the contrary Robinson (1999: Table 1) regarded it as native to East Asia. It has been introduced into South America, Atlantic islands, East Africa, West Indian Ocean islands, South-east Asia, and Pacific islands. It has also been reported from the mid temperate latitudes of the northern hemisphere where it only occurs in greenhouses and hothouses (see Table 2 for details and references). Since these reports are only based on shell identifications, it is not possible to exclude that some are misidentifications (e.g., Muratov 2010: fig. 28).

The genital anatomy of *Opeas* species was investigated by Baker (1945), Baker in Pilsbry (1946), and Gittenberger and van Bruggen (2013). Only three *Opeas* species have been studied: *Opeas hannense* (see Baker 1945: 86, as *Opeas pumilum*), *Opeas pyrgula* (Schmacker & Boettger, 1891) (see Baker 1945: 87; Baker in Pilsbry 1946: 183–184, figs 88 2, 3) and an unidentified species from Misali islet, Zanzibar (see Gittenberger and van Bruggen 2013: 251, fig. 9), but only the anatomy of *Opeas pyrgula* is adequately described. The distal genitalia of the only adult specimen that we have been able to study (Fig. 14) agrees with the general scheme described for these species and in particular with the features reported by Baker (1945) and Baker in Pilsbry (1946) for *Opeas pumilum* and *Opeas pyrgula* and with the description of *Opeas pumilum* given by Baker (1945). The major difference between the two species consists in the swelling between the base of the duct of the bursa copulatrix and the proximal vagina: well developed in *Opeas pyrgula* and much less enlarged in *Opeas pumilum*.

Table 2. Geographical distribution of *Opeas hannense*. Asterisks indicate countries / islands where the species has been recorded only in greenhouses or very disturbed anthropogenic habitats.

Regions	Countries / Islands	References
North America	United States*	Dundee (1974), Nekola (2014)
Central America	Guatemala, Mexico, Nicaragua, and Panama	Thompson (2011)
West Indies	Bahamas, Cuba, Hispaniola, Jamaica, Lesser Antilles (Barbados, Curaçao, Guadeloupe, Martinique, and Saint Martin)	Deisler and Abbott (1984), Chase and Robinson (2001), Rosenberg and Muratov (2006), Espinosa and Ortea (2009), Maceira et al. (2013), Charles (2015), Delannoye et al. (2015), Hovestadt and van Leeuwen (2017), Hovestadt and Neckheim (2020), Espinosa and Robinson (2021)
South America	Argentina, Brazil, Ecuador, Suriname, and Uruguay	van Regteren Altena (1975), Simone (2006), Rumi et al. (2010), Virgillito and Miquel (2013), Miquel and Jaime (2018), Breure et al. (2022a)
Atlantic Ocean	Bermuda, Capo Verde, Saint Helena, and São Tomé	Crowley and Pain (1977), Groh (1983), Bieler and Slapcinsky (2000), Holyoak et al. (2020), Key et al. (2021), Preece et al. (2022)
Europe	Austria*, Czech Republic*, Denmark*, France*, Germany*, Great Britain*, Ireland*, Italy*, Netherlands* and Sweden*	Kerney and Cameron (1979), von Proschwitz (1994), Leiss and Reischütz (1996), Horsák et al. (2004, 2020), Reischütz et al. (2018), Kwitt et al. (2019), Anderson and Rowson (2020), this paper
Africa	Mozambique	Muratov (2010)
Indian Ocean	Madagascar and Seychelles	Gerlach (2006), Bank and Menkhorst (2008), Emberton et al. (2010)
South-East Asia	Singapore	Ho (1995)
Oceania	Pacific Islands (American Samoa, Belau/ Palau, Cook Islands, Federated States of Micronesia, Fiji, French Polynesia, Galapagos Islands, Guam, Hawaii, Pitcairn Islands, Samoa, Solomon Islands, Tonga, and Vanuatu)	Solem (1989), Cowie (2000, 2001), Brook et al. (2010), Brook (2014), Miquel and Herrera (2014), Cowie et al. (2017)

Thus, little continues to be known about the genital anatomy of this genus. We need to ascertain whether the proximal complex of the penis is really undivided, to understand the relationships between the vas deferens and the penial sheath and whether the different structure of the female distal genitalia is due to individual variation or to phylogenetic divergence.

Opeas hannense has only been found in the tropical greenhouse of MUSE, where it is uncommon. This is the first report from Italy.

Paropeas achatinaceum (Pfeiffer, 1846)

Bulimus achatinaceus Pfeiffer, 1846: 82. Type locality: "Java". Type material: lectotype no. ZMB Moll. 65746, Zoological Museum, Berlin (Naggs 1994: fig. 1).

Material examined. Italy • 173 shells and 21 spirit specimens; Padua, Biodiversity Garden (Botanical Garden of Padua); 45°23'52.59"N, 11°52'50.37"E; 06 Mar. 2019; D. Barbato leg.; GMC 57373.

Description. ***Shell*** (Figs 21–24). Dextral, medium in size, minutely perforate to imperforate, elongate, slender, conical, rather robust, pearly off-white, opaque, with 7–9 slightly convex whorls, separated by rather deep and in places irregularly crenulate sutures. Apex obtuse, rounded, and smooth. Last whorl ~ 1/3 of shell height. Aperture small, ~ 1/4 of shell height, obliquely pyriform, slightly prosocline. Peristome interrupted, slightly thickened along outer margin, slightly reflected on columella, with callous rim on parietum and columella; columella straight; outer margin sinuous in lateral view (approximately inverse S-shaped). Protoconch smooth; teleoconch with evident irregular collabral striae. Shell dimensions: SH 9.4–13.1 mm; SD 2.9–3.8 mm; AH 3.0–3.5 mm; AW 1.8–2.2 mm.

Figures 21–24. Shells of *Paropeas achatinaceum* from the Biodiversity Garden (Botanical Garden of Padua), D. Barbato leg. 06 Mar. 2019.

Female distal genitalia (Figs 25, 27). Free oviduct long and wide. Bursa copulatrix sac-like, oval with long slender duct (slightly longer than bursa copulatrix), initially slightly flared, and medially convoluted around free oviduct. Vagina long and wide (longer than free oviduct) with huge proximal lateral bulge containing large ligula.

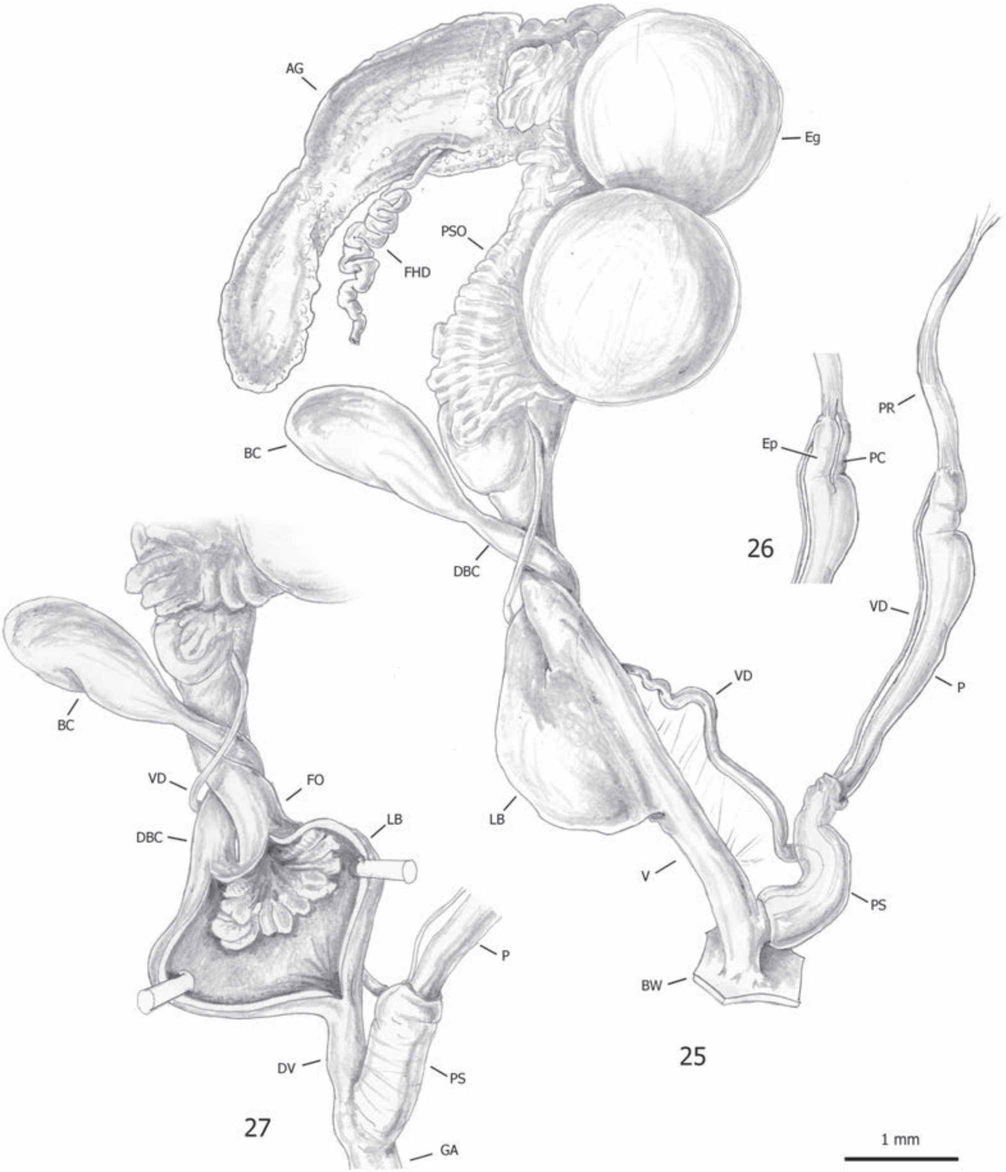
Male distal genitalia (Figs 25–27). Vas deferens of variable diameter (proximal tract narrow, medial tract slightly wider and final tract very narrow), entering penial complex at its proximal end. Penial complex consisting of epiphallus, penial caecum and penis. Epiphallus very short. Penial caecum very short (as long as epiphallus). Penis very long, distinctly divided into proximal and distal parts by difference in calibre; proximal part longer (almost twice distal penis), slender and thin walled; distal penis shorter (half proximal penis), thick, muscular walled and enveloped by penial sheath. Penial retractor muscle bifid, one branch inserted on proximal end of penis, the other branch on tip of penial caecum.

Genital atrium (Figs 25, 27). Short.

Remarks. *Paropeas achatinaceum* is one of the best known subulinids thanks to the excellent anatomical study and the careful taxonomic revision by Naggs (1994). Our anatomical study (Figs 25–27) fully agrees with that of Naggs (1994).

This species is regarded as native to tropical Asia, where it occurs from Nepal and Sri Lanka to South East Asia. Outside this area it is found in Australia and Pacific islands, West Indian Ocean islands, Europe, and the West Asia (see Table 3 for details and references).

The species was found in the Biodiversity Garden (Botanical Garden of Padua), where it forms a well-established population, as in Vienna Zoo, Austria



Figures 25–27. Genital anatomy of *Paropeas achatinaceum* from the Biodiversity Garden (Botanical Garden of Padua), D. Barbato leg. 06 Mar. 2019: **25** genitalia (hermaphrodite gonad excluded) **26** detail of proximal penial complex **27** internal structure of vagina.

Table 3. Geographical distribution of *Paropeas achatinaceum*. Asterisks indicate countries / islands where the species has been recorded only in greenhouses or very disturbed anthropogenic habitats; hash symbol denotes one record based on a specimen of unknown origin recovered from sandy detritus collected on a beach.

Regions	Countries / Islands	References
Europe	Austria*, Italy*, and Malta#	Horsák et al. (2020), Cilia et al. (2022), this paper
West Indian Ocean	Mascarene and Seychelles	Naggs (1994), Griffiths and Florens (2006)
West Asia	Iraq	Hussein et al. (2018)
South Asia	Nepal and Sri Lanka	Naggs (1994), Budha et al. (2015)
South-East Asia	Borneo, Indonesia, and Singapore	Naggs (1994), Schilthuizen and Rutjes (2001), Tan et al. (2015), Nurinsiyaha et al. (2016), Phung et al. (2017)
East Asia	Dongsha Island and Hong Kong	Naggs (1994), Wu et al. (2007)
Oceania	Australia and Pacific islands (American Samoa, Cook Islands, Fiji, French Polynesia, Guam, Hawaii, Northern Mariana Islands, Samoa, and Tonga)	Naggs (1994), Cowie (2000, 2001), Shea (2007), Brook et al. (2010), Stanisic et al. (2010), Kerr and Bauman (2013), Brook (2014), Cowie et al. (2017)

(Horsák et al. 2020). In contrast, the report from Malta is only based on a specimen of unknown origin recovered from sandy detritus collected on a beach (Cilia et al. 2022). This is the first report from Italy and the third from Europe.

Subulina octona (Bruguière, 1789)

Bulimus octonus Bruguière, 1789: 325. Type locality: "… dans les îles Antilles. M. de Badier l'a trouvé abondamment à l'île de la Guadeloupe, & j'en ai vu chez M. d'Antic qui lui ont été envoyés de l'île de Saint-Domingue". Type material: presumed lost (Smith 1992).

Material examined. Italy • 112 shells and 2 spirit specimens; Trento, Tropical greenhouse of the Science Museum of Trento (MUSE); 46°03'45.16"N, 11°06'50.08"E; 04 Jan. 2019; 10 Feb. 2019; 04 May 2019; D. Barbato, G. Bolzonella leg.; GMC 51197 • 29 shells; same locality; 01 Feb. 2022; D. Barbato, A. Benocci leg.; GMC 51188 • 1 shell; same locality; 09 Feb. 2023; D. Barbato, A. Benocci leg.; GMC 57353 • 1 shell; Padua, Biodiversity Garden (Botanical Garden of Padua); 45°23'52.59"N, 11°52'50.37"E; 06 Mar. 2019; D. Barbato leg.; GMC 57374.

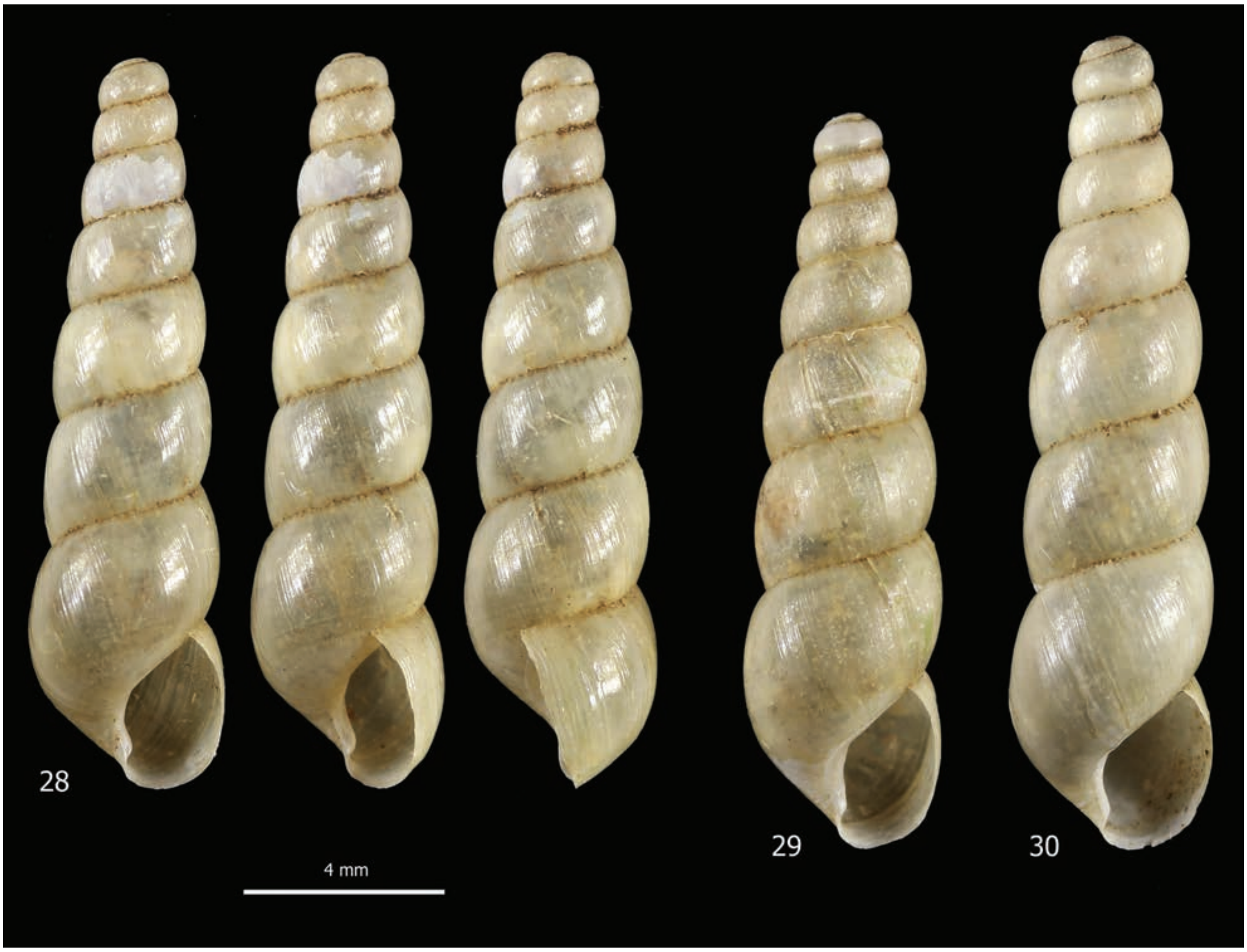
Description. ***Shell*** (Figs 7, 8, 28–30). Shell dextral, medium in size, imperforate, elongate, slender, conical, rather robust, pearly off-white, glossy or waxy and sub-transparent when fresh, with 7–9 slightly convex whorls, separated by rather deep and in places irregularly crenulate sutures. Apex obtuse, rounded, and smooth; last whorl ~ 1/3 of shell height. Aperture small, ~ 1/5 of shell height, ovate, slightly prosocline. Peristome interrupted, not thickened or reflected, with callous rim on parietum and columella; columella concave and obliquely truncate at base; outer margin straight in lateral view. Protoconch smooth; teleoconch with fine, wrinkled, irregular collabral growth lines. Shell dimensions: SH 12.1–16.0 mm; SD 3.3–4.1 mm; AH 2.5–3.2 mm; AW 1.9–2.4 mm.

Female distal genitalia (Fig. 31). Free oviduct very short and wide. Bursa copulatrix sac-like, oval with short slender duct (as long as bursa copulatrix), initially not flared. Vagina very long and slender.

Male distal genitalia (Figs 31, 32). Vas deferens of varying diameter (proximal tract narrow, medial tract slightly wider and final tract very narrow), entering penial complex near proximal end. Penial complex consisting of epiphallus, penial caecum and penis. Epiphallus very short. Penial caecum very short (as long as epiphallus). Penis very long, divided distinctly into proximal and distal parts by difference in calibre, without penial sheath; proximal part longer (twice distal penis), slender and thin walled; distal penis shorter (half proximal penis) and thick, muscular walled. Penial retractor muscle bifid, one branch inserted on tip of penial flagellum, the other branch on tip of penial caecum.

Genital atrium (Fig. 31). Very short.

Remarks. *Subulina octona* is a well-known travelling snail that occurs worldwide (Robinson 1999) but its native range is uncertain. It was described from Guadeloupe and Hispaniola and has been reported as native to tropical America (Pilsbry 1946), the Caribbean (Deisler and Abbott 1984) and Latin America (Robinson 1999) but this was disputed on the grounds that the other species of the genus occur in Africa (Bieler and Slapcinsky 2000). Gerlach (2006) regarded it as native to the Seychelles, based on a subfossil record from Aldabra

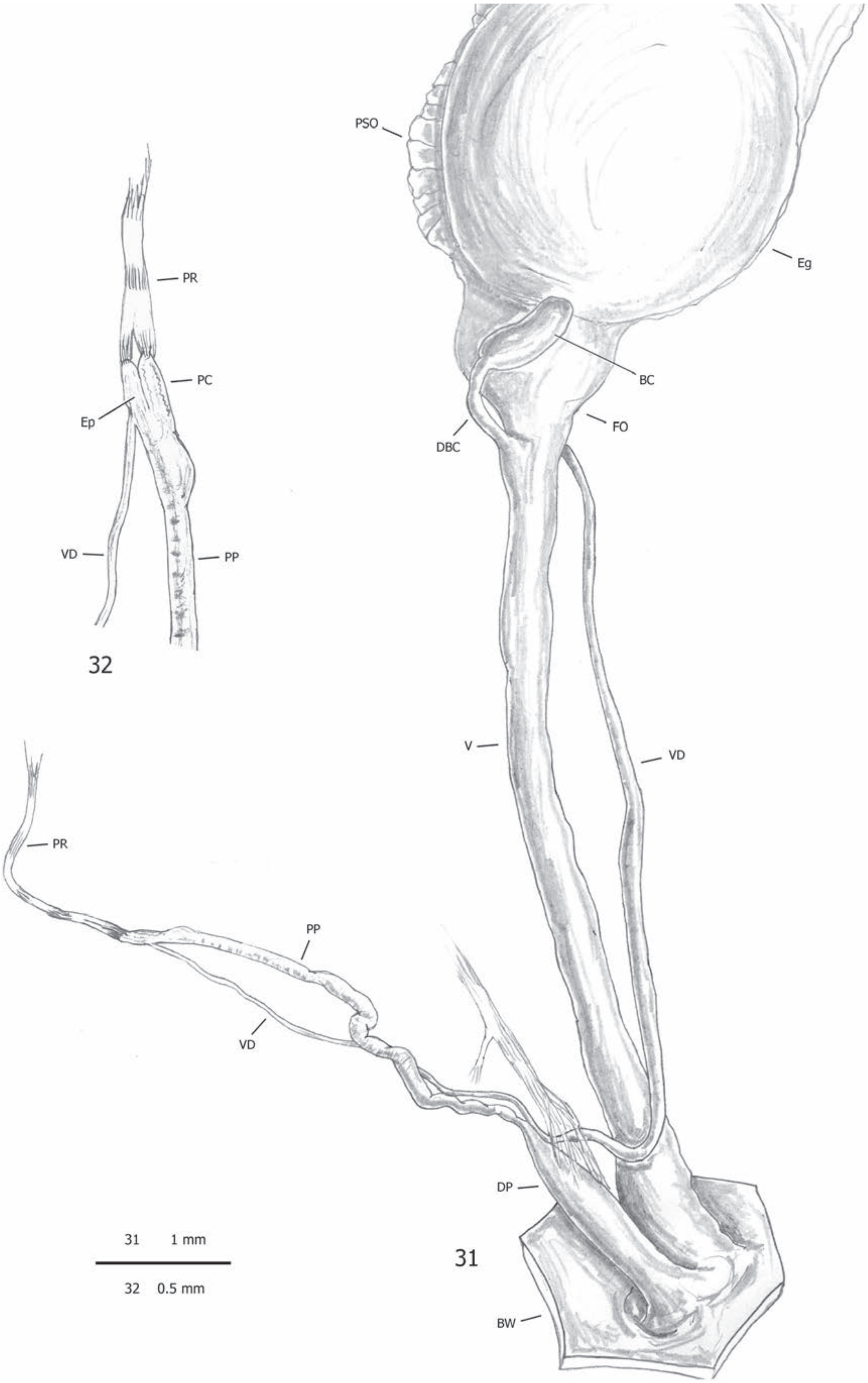


Figures 28–30. Shells of *Subulina octona* from the tropical greenhouse of the Science Museum of Trento (MUSE), D. Barbato & G. Bolzonella leg. 04 Jan. 2019.

reported by Gerlach and van Bruggen (1999). Others suggested that it was originally from tropical America (Griffiths and Florens 2006), south-east Asia (Rumi et al. 2010) or Africa (Breure et al. 2016; Hovestadt and van Leeuwen 2017). Multi-gene phylogenetic analysis of the achatinoid snails by Fontanilla et al. (2017) found that *Subulina octona* and *Subulina striatella* (Rang, 1831) formed a monophyletic group belonging to an unsupported clade including only Old World species, but unfortunately the study included a small selection of subulinine genera, only one of which was from neotropical America.

Subulina octona is now distributed widely in humid tropical and subtropical lowlands across the world. It occurs in Central America, the West Indies, South America, sub-Saharan Africa, West Indian Ocean islands, South, South-East, and East Asia, New Guinea, Australia, and Pacific islands. In the mid temperate latitudes of the northern hemisphere, it only occurs in greenhouses and hothouses (see Table 4 for details and references).

The distal genitalia of MUSE specimens show a general scheme identical to that described by Baker (1927: 3–4, pl. 20, fig. 99), Marcus and Marcus (1968: 189–190) and Araújo and Bessa (1993: 493–495, figs 7–11), but differing in the size of the penial complex from that described by Wiegmann (1894: 214–216, pl. 16, fig. 3; reproduced by Pilsbry 1946: 173, fig. 83h), Schileyko (1999: fig. 662 BC) and Gittenberger and van Bruggen (2013: 250). Instead of a very short penial



Figures 31, 32. Genital anatomy of *Subulina octona* from the tropical greenhouse of the Science Museum of Trento (MUSE), D. Barbato & G. Bolzonella leg. 04 Jan. 2019: **31** genitalia (hermaphrodite gonad excluded) **32** detail of proximal penial complex.

Table 4. Geographical distribution of *Subulina octona*. Asterisks indicate countries / islands where the species has been recorded only in greenhouses or very disturbed anthropogenic habitats.

Regions	Countries / Islands	References
North America	United States*	Dundee (1974), Nekola (2014)
Central America	Belize, Costa Rica, Guatemala, Honduras, Mexico, Nicaragua, Panama, and Salvador	Thompson (2011)
West Indies	Bahamas, Cuba, Hispaniola, Jamaica, and Lesser Antilles (Barbados, Curaçao, Guadeloupe, Martinique, Saint Barthélemy, Saint Martin, and Trinidad)	Deisler and Abbott (1984), Chase and Robinson (2001), Rosenberg and Muratov (2006), Espinosa and Ortea (2009), Robinson et al. (2009), Rutherford (2011), Maceira et al. (2013), Charles (2015), Delannoye et al. (2015), Breure et al. (2016), Herrera-Uria (2016), Hovestadt and van Leeuwen (2017), Hovestadt and Neckheim (2020), Espinosa and Robinson (2021)
South America	Brazil, Columbia, Ecuador, Peru, Suriname, and Venezuela	Baker (1927), Marcus and Marcus (1968), van Regteren Altena (1975), Simone (2006), Rumi et al. (2010), Breure et al. (2022a)
Atlantic Ocean	Bermuda	Bieler and Slapcinsky (2000)
Europe	Austria*, Czech Republic*, Denmark*, Great Britain*, Ireland*, Italy*, Netherlands*, and Sweden*	Kerney and Cameron (1979), von Proschwitz (1994, 2016), Juricková (2006), Da Sois (2015), Reischütz et al. (2018), Anderson and Rowson (2020), Horsák et al. (2020), this paper
Africa	South Africa, Tanzania, and Zimbabwe	van Bruggen (1981), Rowson (2007), Herbert (2010)
Indian Ocean	Aldabra, Madagascar, Maldives, Mascarene, Pemba, and Seychelles	Probst (2001), Gerlach (2006), Griffiths and Florens (2006), Rowson (2007), Emberton and Griffiths (2009), Rowson et al. (2010), Gittenberger and van Bruggen (2013), Gittenberger et al. (2019)
South Asia	India and Sri Lanka	Ranawana (2006), Raheem et al. (2014)
South-East Asia	Indonesia, Peninsular Malaysia, Sabah in Malaysian Borneo, Singapore, and Vietnam	Schileyko (2011), Tan et al. (2015), Foon et al. (2017), Phung et al. (2017), Nurinsiyaha and Hausdorf (2019)
East Asia	Dongsha Islands and Japan*	Minato (1988), Wu et al. (2007)
Oceania	Australia, New Guinea, and Pacific islands (American Samoa, Belau/Palau, Cook Islands, Federated States of Micronesia, Fiji, French Polynesia, Galapagos Islands, Guam, Hawaii, Marshall Islands, New Caledonia, Northern Mariana Islands, Pitcairn Islands, Samoa, Solomon Islands, Tonga, and Vanuatu)	Cowie (2000, 2001), Wiktor (2003), Shea (2007), Brook et al. (2010), Rundell (2010), Stanisic et al. (2010), Brodie and Barker (2012), Kerr and Bauman (2013), Brook (2014), Miquel and Herrera (2014), Cowie et al. (2017)

complex, in agreement with the first description by Baker (1927), MUSE specimens have a long slender penial complex consisting of a short proximal portion (the epiphallus and the penial caecum closely juxtaposed to each other), a long slender medial portion (the proximal penis) and a short swollen distal portion (the distal penis). In particular, based on the male genitalia of a specimen from Dunoon (Guyana) mounted in glycerine jelly and viewed by transmitted light, Baker (1927) described the proximal portion as consisting of a flagellar appendix [the penial caecum] and a very short, thick walled tract [the epiphallus]; the vas deferens entering the penial complex at the proximal end of the epiphallus; the penial retractor joining at the tip of penial caecum; a rather elongate papilla present at the internal opening of the epiphallus into the proximal penis. Baker also described a penial sheath enveloping the distal penis joined by a muscular branch originating from the right lower tentacle retractor; finally he interpreted the structure that Wiegmann (1894) described and figured as the penis as being only the distal penis surrounded by a heavy muscular sheath.

The small size and the very fine structure of the sections of the proximal portion of the penial complex make dissection difficult and differentiation of its components elusive. Our results substantially agree with Baker's description. The differences are: the vas deferens enters the penial complex near the base and not at the tip of the epiphallus; the penial retractor consists of two branches, one joined to the epiphallus, the other to the penial caecum; the small size of the proximal penis makes the penial papilla impossible to detect by stereomicroscope; a classical penial sheath (such as that of *Allopeas* and *Paropeas*) is absent, although a muscular branch from the right lower tentacle retractor joins the distal penis directly on the penial wall. Unfortunately, the scarcity of material prevented a more careful anatomical examination. Some uncertainties about its real organisation and the meaning of such differences among the various anatomical reports therefore remain.

Multi-gene phylogenetic analysis of the achatinoid snails by Fontanilla et al. (2017) found that the genus, as currently conceived, is polyphyletic because the three *Subulina* species examined did not cluster together. The meaning of variation in penis size in *Subulina octona* is also uncertain. Wiegmann (1894) ventured that the extreme reduction of the male distal genitalia was related to "unisexuality" or sequential hermaphroditism (... dass die betreffenden Thiere durch Verkümmerung des männlichen Theils der Genitalien eingeschlechtig geworden sind, oder aber dass die weibliche Geschlechtsreife der männlichen vorausgeht). Others, such as Baker (1927), supposed that the species was a sequential hermaphrodite, but whereas Wiegmann saw it as protogynous, Baker viewed it as protandrous. *Subulina octona* is actually a facultatively self-fertilising egg-retaining species showing no evidence of sequential hermaphroditism (Bessa and Araújo 1995; D'Ávila et al. 2018). Thus the reduced penis may be related to loss of biparental reproduction as already supposed by Wiegmann. However this may be because *Subulina octona* is a complex of species. More research is needed to address these questions.

Subulina octona is common in the tropical greenhouse of MUSE, and has been found in the Biodiversity Garden (Botanical Garden of Padua), where only one specimen was collected. This is the first report from Italy.

Geostilbia aperta **(Swainson, 1840)**

Macrospira aperta Swainson, 1840: 335, fig. 97e, f. Type locality: no locality given; according to Smith (1892: 269), Saint Vincent, Lesser Antilles, West Indies. Type material: unknown. Note: Swainson attributed the new species to the reverend L. Guilding from St. Vincent, from whom he received the material used for the description. Probably this material was accompanied by a manuscript name which Swainson adopted for denoting the species.

Achatina gundlachi Pfeiffer, 1850: 80. Type locality: Cuba. Type material: unknown.

Geostilbia caledonica Crosse, 1867: 186–187, Pl. 7, fig. 4. Type locality: Nouméa, New Caledonia. Type material: 1 syntype in Crosse collection (MNHN-IM-2000-4720) (Breure et al. 2022b).

Material examined. ITALY • 2 shells; Trento, Tropical greenhouse of the Science Museum of Trento (MUSE); 46°03'45.16"N, 11°06'50.08"E; 01 Feb. 2022; D. Barbato, A. Benocci leg.; GMC 51189.

Description. ***Shell*** (Figs 33, 34). Dextral, very small in size, imperforate, elongate, very slender, cylindro-conical, thin and fragile, pearly off-white, colourless,

Figures 33, 34. Shells of *Geostilbia aperta* from the tropical greenhouse of the Science Museum of Trento (MUSE), D. Barbato & A. Benocci leg. 01 Feb. 2022.

glossy and transparent when fresh, ~ 4 slightly convex whorls separated by rather deep sutures. Apex obtuse, rounded, and smooth. Last whorl ~ 2/3 of shell height. Aperture small, ~ 1/3 of shell height, ovate to pyriform, basally flared, slightly prosocline. Peristome interrupted, not thickened or reflected, with callous rim on parietum and columella; columella straight or slightly concave; outer margin slightly arched forward in the middle in lateral view. Protoconch smooth; teleoconch with very fine collabral lines and very fine spiral grooves particularly evident on last whorl. Shell dimensions: SH 2.8 mm; SD 1.0 mm; AH 1.1 mm; AW 0.6 mm.

Body and anatomy. Unknown.

Remarks. The early taxonomy of this land snail revolves around three named species: *Macrospira aperta* Swainson, 1840, *Achatina gundlachi* Pfeiffer, 1850 and *Geostilbia caledonica* Crosse, 1867.

Commenting on the land mollusc species introduced to Saint Helena, Edgar Smith maintained that *Achatina gundlachi* was a junior synonym of *Macrospira aperta* based on examination of Guilding's material from St. Vincent, West Indies, deposited in the British Museum (Smith 1892) and that *Geostilbia caledonica* was also a junior synonym of *Megaspira* [sic] *aperta* (Smith, 1895).

Pilsbry (1908), in his exhaustive revision of orthurethrous snails included in the second edition of the Manual of Conchology, partly rejected Smith's conclusions, regarding *Macrospira aperta* as a species inadequately described and *Geostilbia* as a section of *Cecilioides*. He used *Cecilioides gundlachi* as the valid name for the species. However many years later, dealing with this group again, he adopted *Cecilioides aperta* as the valid name (Pilsbry 1946).

No subsequent authors made any significant contribution for a better taxonomic framework of the species. They repeated what Pilsbry (1946) proposed, believing that a species of *Geostilbia*, sometimes considered a subgenus or a synonym of *Cecilioides*, could be found almost everywhere in the world, having spread from the Mesoamerican area (e.g., Robinson 1999). Indeed many consider it native to the West Indies, Neotropics or Caribbean basin (Dundee 1974; Cowie 1997; Robinson 1999; Chase and Robinson 2001; Rosenberg and Muratov 2006; Thompson 2011; Miquel and Herrera 2014; Nurinsiyaha et al. 2016; Nurinsiyaha and Hausdorf 2019). Others report it to be native to southern Europe (Cotton 1954) or North America north of Mexico (Nekola 2014).

A species, sometimes named *Geostilbia aperta* (or *Cecilioides aperta*), *Geostilbia caledonica* (or *Cecilioides caledonica*) or *Geostilbia gundlachi* (or *Cecilioides gundlachi*), is currently reported from North, Central and South America, the Caribbean and the Indo-Pacific Region from South-East Asia to Hawaii and Cook Islands (see Table 5 for details and references). It has also been reported from Saint Helena (Smith 1892) based on a misidentification of *Cecilioides acicula* (Crowley and Pain 1977), and from Barbados, Curaçao and Galapagos, where it was no longer found in recent field surveys (Chase and Robinson 2001; Miquel and Herrera 2014; Hovestadt and van Leeuwen 2017).

It is difficult to say anything new about this group of species, since there is no anatomical data. We can rely on shell characters, the most interesting of which are the spiral sculpture particularly evident in the last whorl, the non-truncated or slightly truncated columella and the basally flared aperture. Based on a close resemblance to *Cecilioides*, the species of *Geostilbia* have been placed in the family Ferussaciidae but this similarity could also be due to convergence: true *Cecilioides* have no microsculpture on the teleoconch, have a truncated columella and have no basally flared aperture. In their phylogenetic analysis of the achatinoideans Fontanilla et al. (2017) examined a *Cecilioides* species – *Cecilioides gokweana* (Boettger, 1870) – which may actually be *Geostilbia*, if the material investigated, collected by DG Herbert, matches the description of this species given by him (cf. Herbert 2010: 127 for description and figure). If this is confirmed, *Geostilbia* does not belong to the Ferussaciidae but to a distinct group of Achatinidae. This of course does not resolve the relationships between *Cecilioides* and *Geostilbia*: *Cecilioides* may really belong to the Ferussaciidae or to the same or a different group of Achatinidae, which may include *Geostilbia*.

MolluscaBase lists eight *Geostilbia* species (MolluscaBase eds 2024c), but except for the widespread *Geostilbia aperta* and the south American *Geostilbia blandiana* Crosse, 1880, all the others occur from Madagascar to Southeast

Table 5. Geographical distribution of *Geostilbia aperta*. Asterisks indicate countries / islands where the species has been recorded only in greenhouses or very disturbed anthropogenic habitats.

Regions	Countries / Islands	References
North America	United States*	Pilsbry (1946), Dundee (1974), Nekola (2014)
Central America	Nicaragua	Thompson (2011)
West Indies	Cuba, Hispaniola, Jamaica, Lesser Antilles (Guadeloupe, Martinique, Saint Martin, and Saint Vincent)	Smith (1892), Rosenberg and Muratov (2006), Maceira et al. (2013), Charles (2015), Hovestadt and Neckheim (2020), Espinosa and Robinson (2021)
South America	Brazil	Simone (2006)
South-East Asia	Indonesia, Peninsular Malaysia, and Philippines	Vermeulen and Whitten (1998), Maassen (2001), Groh (2015), Nurinsiyaha et al. (2016), Foon et al. (2017), Nurinsiyaha and Hausdorf (2019)
Oceania	Australia, New Guinea, and Pacific Islands (Cook Islands, Guam, Hawaii, and New Caledonia)	Solem (1964), van Benthem Jutting (1964), Cowie (2000, 2001), Shea (2007), Stanisic et al. (2010)

Asia. There is great uncertainty about species-level taxonomy of *Geostilbia*. Some of the species listed by MolluscaBase may prove to be true *Cecilioides* based on the apparent absence of spiral microsculpture, truncated columella and not basally flared aperture: this could be true of *Geostilbia philippinica* von Möllendorff, 1890 and *Geostilbia sheilae* Groh, 2015 (see Groh 2015). On the other hand, some species reported as *Cecilioides* by MolluscaBase, such as the East African *Cecilioides callipeplum* (Connolly, 1923), for which clear spiral sculpture is reported by Verdcourt (1986), van Bruggen and van Goethem (2001), and van Bruggen (2008), or the South African *Cecilioides gokweana*, for which clear spiral sculpture is described by Herbert (2010), may prove to be true *Geostilbia*.

We assign two shells found in the litter of the tropical greenhouse of MUSE to this species (unfortunately no living specimen was found during our collecting). This is the first report of the species from Europe.

Acknowledgements

We thank the staff of MUSE (Trento, Italy), in particular Francesca Rossi for permission and assistance during sampling and Andrea Bianchi for information on the flora of the Afromontane greenhouse. We also thank the staff of the Botanical Garden of Padua, especially Barbara Baldan for authorisation to visit the greenhouses and Roberto Tacchetto for assistance during field sampling. Special thanks also to Gregorio Bolzonella (Siena, Italy) for help during collecting, Sigrid Hof (Frankfurt am Main, Germany) for loan of specimens from Senckenberg Forschungsinstitut, Giovanni Cappelli (Siena, Italy) for photographs of the shells, and Helen Ampt (Siena, Italy) for English language revision.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

D. Barbato and G. Manganelli were funded under the National Recovery and Resilience Plan (NRRP), Mission 4 Component 2 Investment 1.4 - Call for tender No. 3138 of 16 December 2021, rectified by Decree n.3175 of 18 December 2021 of Italian Ministry of University and Research funded by the European Union – NextGenerationEU; Award Number: Project code CN_00000033, Concession Decree No. 1034 of 17 June 2022 adopted by the Italian Ministry of University and Research, CUP B63C22000650007 Project title “National Biodiversity Future Center - NBFC”.

Author contributions

Conceptualisation: DB and GM; Methodology, Formal analysis, Investigation, Data Curation: AB, DB, FG, and GM; Writing - Original draft & Writing - Review and Editing: AB, DB, FG, and GM; Supervision: GM; Funding Acquisition: GM.

Author ORCIDs

Giuseppe Manganelli https://orcid.org/0000-0002-8453-280X
Andrea Benocci https://orcid.org/0000-0003-3145-215X
Debora Barbato https://orcid.org/0000-0003-1105-1711
Folco Giusti https://orcid.org/0000-0001-8722-4653

Data availability

All of the data that support the findings of this study are available in the main text.

References

Anderson R, Rowson B (2020) Annotated list of the non-marine Mollusca of Britain and Ireland. https://conchsoc.org/sites/default/files/MolluscWorld/Anderson-2008.pdf [Accessed on 02.02.2023]

Anonymous (undated) Spiked awl snail *Allopeas clavulinum* (Potiez & Michaud, 1838) (Gastropoda: Subulinidae). https://www.smsl.co.nz/site/southernmonitoring/files/NZB/Other/Spiked%20Awl%20Snail%20Allopeas%20clavulinum_May2017.pdf [Accessed on 13.04.2023]

Araújo JDB, Bessa EDA (1993) Moluscos de importância econômica no Brasil. II Subulinidae, *Subulina octona* (Bruguière) (Mollusca, Gastropoda, Pulmonata, Stylommatophora). Revista Brasileira de Zoologia 10(3): 489–497. https://doi.org/10.1590/S0101-81751993000300016

Baker HB (1927) The Mollusca collected by the University of Michigan-Williamson Expedition in Venezuela. Part V. Occasional Papers of the Museum of zoology – University of Michigan 182: 1–36[, pls. 20–26].

Baker HB (1945) Some American Achatinidae. The Nautilus 58: 84–92. https://doi.org/10.5962/bhl.part.27492

Bank RA, Menkhorst HPMG (2008) Notes on the nomenclature of some land- and freshwater molluscs of the Seychelles, with consequences for taxa from Africa, Madagascar, India, the Philippines, Jamaica, and Europe. Basteria 72: 93–110.

Bergey EA, Figueroa LL, Mather CM, Martin RJ, Ray EJ, Kurien JT, Westrop DR, Suriyawong P (2014) Trading in snails: Plant nurseries as transport hubs for non-native species. Biological Invasions 16(7): 1441–1451. https://doi.org/10.1007/s10530-013-0581-1

Bessa ECA, Araújo JLB (1995) Ocorrência de autofecundação em *Subulina octona* (Brugüière) (Pulmonata, Subulinidae) em condições de laboratório. Revista Brasileira de Zoologia 12(3): 719–723. https://doi.org/10.1590/S0101-81751995000300025

Bieler R, Slapcinsky J (2000) A case study for the development of an island fauna: recent terrestrial mollusks of Bermuda. Nemouria Occasional Papers of the Delaware Museum of Natural History 44: 1–100.

Boettger O (1870) Ueber den Mergel vom Gokwe in Südafrika und seine Fossilien. Bericht über die Tätigkeit des Offenbacher Vereins für Naturkunde 11: 45–50.

Bouchet P, Rocroi J-P (2005) Classification and nomenclator of gastropod families. Malacologia 47(1–2): 1–397. https://doi.org/10.4002/040.061.0201

Bouchet P, Rocroi J-P, Hausdorf B, Kaim A, Kano Y, Nützel A, Parkhaev P, Schrödl M, Strong EE (2017) Revised classification, nomenclator and typification of gastropod and monoplacophoran families. Malacologia 61(1–2): 1–526. https://doi.org/10.4002/040.061.0201

Bourguignat JR (1883) Histoire malacologique de l'Abyssinie. Annales des Sciences Naturelles, Zoologie, ser. 6, 15(Art. 2): 1–162[, pls. 7–10].

Breure B, Hovestadt A, Fields A, Robinson D (2016) The land Mollusca (Gastropoda) of Saint Kitts and Nevis (Lesser Antilles), with description of a new species. The Nautilus 130: 27–52.

Breure ASH, Roosen MT, Ablett JD (2022a) Land and freshwater molluscs of mainland Ecuador: An illustrated checklist. Iberus: Revista de la Sociedad Espanola de Malacologia 40: 1–290.

Breure ASH, Salvador A, Ablett JD (2022b) New taxa introduced in Mollusca and Brachiopoda. In: Breure ASH, Audibert C, Ablett JD (Eds) Joseph Charles Hippolyte Crosse (1826–1898): 1, biography, bibliography and new taxa introduced. Royal Belgian Institute of Natural Sciences, Bruxelles, 43–298.

Brodie G, Barker GM (2012) *Subulina octona* (Bruguière, 1789). Family Subulinidae. 'USP Introduced Land Snails of the Fiji Islands. Fact Sheet Series', No. 8.

Brook FJ (2014) Land snails of Vava'u. In: Atherton JN, McKenna SA, Wheatley A (Eds) Rapid biodiversity assessment of the Vava'u Archipelago, Kingdom of Tonga. Secretariat of the Pacific regional environment Programme, Apia, Samoa, 79–91.

Brook FJ, Walter RK, Craig JA (2010) Changes in the terrestrial molluscan fauna of Miti'āro, southern Cook Islands. Tuhinga 21: 75–98.

Bruguière JG (1789–1792) Encyclopédie méthodique ou par ordre de matières. Histoire naturelle des vers, volume 1. Pancoucke, Paris, [xviii +] 344 pp. https://doi.org/10.5962/bhl.title.53769

Budha PB, Naggs F, Backeljau T (2015) Annotated Checklist of the Terrestrial Gastropods of Nepal. ZooKeys 492: 1–48. https://doi.org/10.3897/zookeys.492.9175

Charles L (2015) Mollusques terrestres de l'archipel de la Guadeloupe, Petites Antilles. Rapport d'inventaire 2014–2015. DEAL Guadeloupe, 88 pp[, 11 pls + annexes].

Chase R, Robinson DG (2001) The uncertain history of land snails on Barbados: Implications for conservation. Malacologia 43: 33–57.

Cilia DP, Nappo A, Cardona S (2022) Contributions to the malacology of Malta, IV & V: Second European record of *Paropeas achatinaceum* (L. Pfeiffer, 1846) (Gastropoda, Achatinidae) and an annotated checklist of allochthonous non-marine gastropods. Bollettino Malacologico 58(2): 126–142. https://doi.org/10.53559/BollMalacol.2022.15

Connolly M (1923) Notes on African non-marine Mollusca, with descriptions of many new species. The Annals and Magazine of Natural History 12(72): 633–659[, pl. 19]. https://doi.org/10.1080/00222932308632989

Cotton BC (1954) A catalogue of introduced snails and slugs in Australia. Records of the South Australian Museum 11: 177–187.

Cowie RH (1997) Catalog and bibliography of the nonindigenous nonmarine snails and slugs of the Hawaiian Islands. Bishop Museum Occasional Papers 50: 1–66.

Cowie RH (2000) Non-indigenous land and freshwater molluscs in the islands of the Pacific: conservation impacts and threats. In: Sherley G (Ed.) Invasive Species in The Pacific: A Technical Review and Regional Strategy. South Pacific Regional Environment Programme, Apia, 143–172.

Cowie RH (2001) Invertebrate invasions on Pacific Islands and the replacement of unique native faunas: A synthesis of the land and freshwater snails. Biological Invasions 3(2): 119–136. https://doi.org/10.1023/A:1014529019000

Cowie RH, Hayes KA, Tran CT, Meyer WM III (2008) The horticultural industry as a vector of alien snails and slugs: Widespread invasions in Hawaii. International Journal of Pest Management 54(4): 267–276. https://doi.org/10.1080/09670870802403986

Cowie RH, Rundell RJ, Yeung NW (2017) Samoan land snails and slugs. An identification guide. Pago Pago, American Samoa. Department of Marine and Wildlife Resources, American Samoa Government, Contribution (Pacific Biological Survey), no. 2017-004, [viii +] 71 pp.

Crosse H (1867) Description d'un genre nouveau et de plusieurs espèces inédites provenant de la Nouvelle-Calédonie. Journal de Conchyliologie 15(2): 177–194[, pls 5, 7].

Crosse H (1880) Diagnoses Molluscorum novorum, in insula "Nossibé" dicta et in provincia Paraensis collectorum. Journal de Conchyliologie 28(2): 149–150.

Crowley TE, Pain T (1977) Mollusca not Charopidae. In: Basilewsky P. (Ed.) La Faune Terrestre de l'Île de Sainte-Hélène. Quatrième partie. Annales du Musée Royal de l'Afrique Centrale, Sciences Zoologiques 220: 534–575.

d' Orbigny AD (1838) Voyage dans l'Amérique méridionale (le Brésil, la république orientale de l'Uruguay, la République argentine, la Patagonie, la république du Chili, la république de Bolivia, la république du Pérou), exécuté pendant les années 1826, 1827, 1828, 1829, 1830, 1831, 1832 et 1833. Vol. 5(3) Mollusques, Livraison 32: 233–280[, pl. 47].

D'Ávila S, Medeiros C, Vargas T, de Mendonça CLF (2018) Life history of *Subulina octona* (Brugüière) (Gastropoda: Pulmonata: Subulinidae) based on four-year laboratory observations and a comparative histological analysis of egg-retaining and ovoviviparous subulinids. Journal of Natural History 52(23–24): 1551–1569. https://doi.org/10.1080/00222933.2018.1478996

Da Sois L (2015) Greenhouse gastropods of the Hortus botanicus Leiden (distribution) and other experiences in the Botanical Garden. Bachelor Thesis, University of Padova, Padova, Italy. http://tesi.cab.unipd.it/61106/1/Bacheor_thesis_Luca_Da_Sois.pdf [Accessed on 12.11.2023]

Deisler JE, Abbott RT (1984) Range extensions of some introduced land mollusks in the Bahama Islands, with first reports for four species. The Nautilus 98(1): 12–17.

Delannoye R, Charles L, Pointier J-P, Massemin D (2015) Mollusques continentaux de la Martinique. Non-marine Molluscs of Martinique, Lesser Antilles. Biotope, Mèze, Muséum national d'Histoire naturelle, Paris [collection Inventaires et biodiversité], 328 pp.

Dundee DS (1974) Catalog of introduced molluscs of eastern North America (North of Mexico). Sterkiana 55: 1–37.

Emberton KC, Griffiths OL (2009) Pulmonate land mollusks from three rainforest transects in northeastern Madagascar: part 1 of 2, with descriptions of 12 new species and one new subspecies: (Gastropoda: Pulmonata). Archiv für Molluskenkunde der Senckenbergischen Naturforschenden Gesellschaft 138(2): 137–167. https://doi.org/10.1127/arch.moll/1869-0963/138/137-167

Emberton CK, Slapcinsky J, Campbell CA, Rakotondrazafy JA, Andriamiarison TN, Emberton JD (2010) Terrestrial mollusks of Andriantantely Massif, eastern Madagascar, with descriptions of 36 new species (Gastropoda: Caenogastropoda: Pulmonata). Archiv für Molluskenkunde 139(1): 71–141. https://doi.org/10.1127/arch.moll/1869-0963/139/071-141

Espinosa J, Ortea J (2009) Moluscos terrestres de Cuba. UPC Print, Vasa, Finland, 191 pp.

Espinosa JA, Robinson DG (2021) Annotated checklist of the terrestrial mollusks (Mollusca: Gastropoda) from Hispaniola Island. Novitates Caribaea 17(17): 71–146. https://doi.org/10.33800/nc.vi17.250

Férussac AEJPJF d'Audebard (1814) Mémoires géologiques sur les terreins formés sous l'eau douce par les débris fossiles des mollusques vivant sur la terre ou dans l'eau non salée. Poulet, Paris, 76 pp.

Férussac AEJPJF d'Audebard (1821) Tableaux systématiques des animaux mollusques suivis d'un Prodrome géneral pour tous les mollusques terrestres ou fluviatiles vivantes ou fossiles. Livraison 11: 49–72 [Quarto edition]. Baillière, Paris.

Fischer P, Crosse H (1877) Études sur les Mollusques terrestres et fluviatiles du Mexique et du Guatemala. Mission scientifique au Mexique et dans l'Amérique Centrale. Recherches zoologiques, Partie 7. Vol. 1, Livraison 6: 547–624[, pls. 25–28]. Imprimerie Nationale, Paris.

Fontanilla IK, Naggs F, Wade CM (2017) Molecular phylogeny of the Achatinoidea (Mollusca: Gastropoda). Molecular Phylogenetics and Evolution 114: 382–385. https://doi.org/10.1016/j.ympev.2017.06.014

Foon JK, Clements GR, Liew T-S (2017) Diversity and biogeography of land snails (Mollusca, Gastropoda) in the limestone hills of Perak, Peninsular Malaysia. ZooKeys 682: 1–94. https://doi.org/10.3897/zookeys.682.12999

Gerber J, Clark SA (2015) First record of the predatory land snail *Streptostele* (*Tomostele*) *musaecola* (Pulmonata: Streptaxidae) in the continental United States. American Conchologist 43(2): 26–28.

Gerlach J (2006) Terrestrial and freshwater Mollusca of the Seychelles Islands. Backhuys, Leiden, 141 pp.

Gerlach J, van Bruggen AC (1999) Streptaxidae (Mollusca: Gastropoda: Pulmonata) of the Seychelles Islands, western Indian Ocean. Zoologische Verhandelingen Leiden 328: 1–60[, pl. 1].

Girard AA (1895) Sur le "*Thyrophorella thomensis*", Greeff, gastéropode terrestre muni d'un faux opercule à charnière. Jornal de Sciencias Mathematicas, Physicas e Naturaes [Lisboa], ser. 2, 4: 28–32[, 1 pl.].

Gittenberger E, van Bruggen AC (2013) Land snails of the islet of Misali, off Pemba Island, Zanzibar, Tanzania. Zoologische Mededelingen Leiden 87(3): 235–273.

Gittenberger E, Reijnen BT, Groenenberg DSJ (2019) Terrestrial gastropods of the Maldives, all of which are invasive? Journal of Conchology 43: 353–383.

Godwin-Austen HH (1920) Land and freshwater Mollusca of India, including South Arabia, Baluchistan, Afghanistan, Kashmir, Nepal, Burmah, Pegu, Tenasserim, Malay Peninsula, Ceylon, and other islands of the Indian Ocean. Supplementary to Messrs. Theobald and Hanley's Conchologia Indica. Taylor & Francis, London, Vol. 3, part 1: 1–65[, pls 159–165].

Griffiths OL, Florens VFB (2006) A field guide to the non-marine molluscs of the Mascarene Islands (Mauritius, Réunion and Rodrigues) and the northern dependencies of Mauritius. Bioculture Press, Mauritius, 188 pp.

Groh K (1983) Revision der Land- und Süsswassergastropoden der Kapverdischen Inseln. Archiv für Molluskenkunde 113: 159–223.

Groh K (2015) The Ferussaciidae (Gastropoda, Pulmonata) of the Philippines, with the description of a new *Geostilbia* from Cebu. Visaya 4(3): 73–86.

Herbert DG (2010) The introduced terrestrial Mollusca of South Africa. SANBI Biodiversity Series 15. South African National Biodiversity Institute, Pretoria, 108 pp.

Herrera-Uria J (2016) A checklist of terrestrial molluscs (Mollusca: Gastropoda) from Sierra Bibijagua, Isla de la Juventud, Cuba. Check List 12(5): 1968. https://doi.org/10.15560/12.5.1968

Heywood VH (2011) The role of botanic gardens as resource and introduction centres in the face of global change. Biodiversity and Conservation 20(2): 221–239. https://doi.org/10.1007/s10531-010-9781-5

Ho WH (1995) A review of the land-snail fauna of Singapore. The Raffles Bulletin of Zoology 43: 91–113.

Holyoak DT, Holyoak GA, Lima RFD, Panisi M, Sinclair F (2020) A checklist of the land Mollusca (Gastropoda) of the islands of São Tomé and Príncipe, with new records and descriptions of new taxa. Iberus : Revista de la Sociedad Espanola de Malacologia 38: 219–319.

Horsák M, Dvořák L, Juřičková L (2004) Greenhouse gastropods of the Czech Republic: Current stage of research. Malacological Newsletter 22: 141–147.

Horsák M, Naggs F, Backeljau T (2020) *Paropeas achatinaceum* (Pfeiffer, 1846) and other alien subulinine and opeatine land snails in European greenhouses (Gastropoda, Achatinidae). Malacologia 63(1): 123–130. https://doi.org/10.4002/040.063.0112

Hovestadt A, Neckheim CM (2020) A critical checklist of the non-marine molluscs of St.Martin, with notes on the terrestrial malacofauna of Anguilla and Saint-Barthélemy, and the description of a new subspecies. Folia Conchyliologica 57: 1–38.

Hovestadt A, van Leeuwen S (2017) Terrestrial molluscs of Aruba, Bonaire and Curaçao in the Dutch Caribbean: An updated checklist and guide to identification. Vita Malacologica 16: 1–39.

Hulme PE (2009) Trade, transport and trouble: Managing invasive species pathways in an era of globalization. Journal of Applied Ecology 46(1): 10–18. https://doi.org/10.1111/j.1365-2664.2008.01600.x

Hulme PE (2015) Resolving whether botanic gardens are on the road to conservation or a pathway for plant invasions. Conservation Biology 29(3): 816–824. https://doi.org/10.1111/cobi.12426

Hulme PE (2021) Unwelcome exchange: International trade as a direct and indirect driver of biological invasions worldwide. One Earth 4(5): 666–679. https://doi.org/10.1016/j.oneear.2021.04.015

Hussein IA, Aldoori NL, Aldoori ML (2018) Sequencing of mitochondrial COI gene in new Iraqi record *Paropeas achatinaceum* L. P. Feiffer, 1846, Gastropoda: Subulinidea. Research Journal of Pharmacy and Technology 11(10): 4267–4271. https://doi.org/10.5958/0974-360X.2018.00782.5

Hutton T (1834) On the land shells of India. Journal of the Asiatic Society of Bengal 3(26): 81–93.

Jaskuła R, Sulikowska-Drozd A, Jablonska A, Banas K, Rewicz T (2019) Undesirable immigrants: Hobbyist vivaria as a potential source of alien invertebrate species. PeerJ 7: e7617. https://doi.org/10.7717/peerj.7617

Juricková L (2006) *Subulina octona* (Bruguière, 1798) – a new greenhouse species for the Czech Republic (Mollusca: Gastropoda: Subulinidae). Malacologica Bohemoslovaca: Journal About Molluscs in Central Europe 5: 1–2. https://doi.org/10.5817/MaB2006-5-1

Keller RP, Geist J, Jeschke JM, Kühn I (2011) Invasive species in Europe: Ecology, status, and policy. Environmental Sciences Europe 23(1): 23. https://doi.org/10.1186/2190-4715-23-23

Kenis M, Auger-Rozenberg MA, Roques A, Timms LL, Péré C, Cock MJW, Settele J, Augustine F, Lopez Vaamonde C (2009) Ecological effects of invasive alien insects. Biological Invasions 11(1): 21–45. https://doi.org/10.1007/s10530-008-9318-y

Kerney MP, Cameron RAD (1979) A field guide to the land snails of Britain and north-west Europe. Collins, London, 288 pp.

Kerr AM, Bauman S (2013) Annotated checklist of the land snails of the Mariana Islands, Micronesia. University of Guam Marine Laboratory Technical Report 148, [vii +] 72 pp.

Key R, Fowler L, Pryce D (2021) Terrestrial & freshwater invertebrates of St Helena. Pisces publications for St. Helen Nature Conservation Group, 220 pp.

Kolicka M, Dziuba MK, Zawierucha K, Kuczyńska-Kippen N, Kotwicki L (2015) Palm house – biodiversity hotspot or risk of invasion? Aquatic invertebrates: The special case of Monogononta (Rotifera) under greenhouse conditions. Biologia 70(1): 94–103. https://doi.org/10.1515/biolog-2015-0012

Kwitt S, Patzner RA, Reischütz S, Reischütz PL (2019) Die Ergebnisse einer Untersuchung der terrestrischen Molluskenfauna der Gewächshäuser des botanischen Gartens der Universität Salzburg. Nachrichtenblatt der Ersten Vorarlberger Malakologischen Gesellschaft 26: 69–74.

Leiss A, Reischütz PL (1996) Ein Beitrag zur Kenntnis der Molluskenfauna der Gewächshäuser in Wien und Niederösterreich. Wissenschaftliche Mitteilungen Niederösterreichisches Landesmuseum 9: 173–184.

Maassen WJM (2001) A preliminary checklist of the non-marine molluscs of West Malaysia. De Kreukel (extra edition 2001) 2001: 1–155.

Maceira D, Miquel SE, Espinosa J, Virgillito M, Lauranzón B (2013) Moluscos terrestres exóticos y primera cita de la familia Punctidae (Mollusca: Pulmonata: Gastropoda) y de su especie *Paralaoma servilis* para Cuba. Solenodon 11: 95–102.

Manganelli G, Lesicki A, Benocci A, Barbato D, Miserocchi D, Pienkowska JR, Giusti F (2022) A small slug from a tropical greenhouse reveals a new rathouisiid lineage with triaulic tritrematric genitalia (Gastropoda: Systellommatophora). Zoological Journal of the Linnean Society 197(1): 76–103. https://doi.org/10.1093/zoolinnean/zlac054

Marcus E, Marcus E (1968) Über einige Subulinidae (Pulmonata von Sao Paulo). Beiträge zur Neotropischen Fauna 5(3): 186–208. https://doi.org/10.1080/01650526809360407

Maynard GV, Lepschi BJ, Malfroy SF (2018) Norfolk Island quarantine survey 2012–2014 – a comprehensive assessment of an isolated subtropical island. Proceedings of the Linnean Society of New South Wales 140: 7–243.

Mienis HK, Rittner O, Vaisman S (2012) The spike awlsnail *Lamellaxis clavulinus* in Israel. Tentacle 20: 15–16.

Miller JS (1822) A list of the freshwater and landshells occurring in the environment of Bristol, with observations. Annals of Philosophy 3(17): 376–381. [New Series]

Minato H (1988) A systematic and bibliographic list of the Japanese land snails. Society for the publication of a systematic and bibliographic list of the Japanese land snails, Shirahama, [x +] 294 pp[, 7 pls].

Miquel SE, Herrera HW (2014) Catalogue of terrestrial gastropods from Galápagos (except Bulimulidae and Succineidae) with description of a new species of *Ambrosiella* Odhner (Achatinellidae) (Mollusca: Gastropoda). Archiv für Molluskenkunde 143(2): 107–133. https://doi.org/10.1127/arch.moll/1869-0963/143/107-133

Miquel SE, Jaime GL (2018) Subulinidae snails from northern Argentina with description of a new species of *Nannobeliscus* Weyrauch (Gastropoda, Stylommatophora, Achatinoidea). Spixiana 41: 1–7.

Möllendorff OF von (1890) Die Landschnecken-Fauna der Insel Cebu. Bericht über die Senckenbergische Naturforschende Gesellschaft in Frankfurt-am-Main (1890): 189–292[, pls 7–9]. https://doi.org/10.5962/bhl.title.13047

MolluscaBase eds (2024a) *Cecilioides* A. Férussac, 1814. MolluscaBase. [Accessed at] https://www.molluscabase.org/aphia.php?p=taxdetails&id=819997 [on 2024-03-06]

MolluscaBase eds (2024b) *Allopeas clavulinum* (Potiez & Michaud, 1838). MolluscaBase. [Accessed at] https://www.molluscabase.org/aphia.php?p=taxdetails&id=875197 [on 2024-03-06]

MolluscaBase eds (2024c) *Geostilbia* Crosse 1867. MolluscaBase. [Accessed at] https://www.molluscabase.org/aphia.php?p=taxdetails&id=833808 [on 2024-03-06]

Mörch OAL (1864) Fortegnelse over de i Danmark forekommende Land- og Ferskvandsbløddyr.Videnskabelige Meddelelser fra den Naturhistorisk Forening i Kjobenhavn, 17–22(for 1863): 265–367.

Muratov IV (2010) Terrestrial molluscs of Cabo Delgado and adjacent inland areas of North-Eastern Mozambique. African Invertebrates 51(2): 255–288. https://doi.org/10.5733/afin.051.0203

Naggs F (1994) The reproductive anatomy of *Paropeas achatinaceum* and a new concept of *Paropeas* (Pulmonata: Achatinoidea: Subulinidae). The Journal of Molluscan Studies 60(2): 175–191. https://doi.org/10.1093/mollus/60.2.175

Nekola JC (2014) Overview of the North American terrestrial gastropod fauna. American Malacological Bulletin 32(2): 225–235. https://doi.org/10.4003/006.032.0203

Nordsieck H (1986) The system of the Stylommatophora (Gastropoda), with special regard to the systematic position of the Clausiliidae, II. Importance of the shell and distribution. Archiv für Molluskenkunde 117(1–3): 93–116.

Noseworthy RG, Lim N-R, Choi K-S (2007) A Catalogue of the Mollusks of Jeju Island, South Korea. The Korean Journal of Malacology 23: 65–104.

Nurinsiyaha AS, Hausdorf B (2019) Listing, impact assessment and prioritization of introduced land snail and slug species in Indonesia. The Journal of Molluscan Studies 85(1): 92–102. https://doi.org/10.1093/mollus/eyy062

Nurinsiyaha AS, Fauzia H, Hennig C, Hausdorf B (2016) Native and introduced land snail species as ecological indicators in different land use types in Java. Ecological Indicators 70: 557–565. https://doi.org/10.1016/j.ecolind.2016.05.013

Osorio CR (2018) Lista de los moluscos de Isla de Pascua (Rapa Nui) Chile, en el Pacifico Sur. Boletín del Museo Nacional de Historia Natural 67(1): 55–80. https://doi.org/10.54830/bmnhn.v67.n1.2018.37

Parcon JA, Lit Jr IL, Camacho MVC, de Chavez ERC (2020) Diversity of land snails in the karst areas of Sta. Teresita, Cagayan province, Luzon island with notes on new distribution records. Philippine Journal of Science 150(S1): 525–537. https://doi.org/10.56899/150.S1.39

Pergl J, Pyšek P, Bacher S, Essl F, Genovesi P, Harrower CA, Hulme PE, Jeschke JM, Kenis M, Kühn I, Perglová I, Rabitsch W, Roques A, Roy DB, Roy HE, Vilà M, Winter M, Nentwig W (2017) Troubling travellers: Are ecologically harmful alien species associated with particular introduction pathways? NeoBiota 32: 1–20. https://doi.org/10.3897/neobiota.32.10199

Pfeiffer L (1840) Uebersicht der im Januar, Februar und März, 1839 auf Cuba gesammelten Mollusken. Archiv für Naturgeschichte 6: 250–264.

Pfeiffer L (1846) Symbolae ad historiam Heliceorum. Sectio tertia. Th. Fischer, Cassellis, 100 pp.

Pfeiffer L (1850) Beschreibungen neuer Landschnecken. Zeitschrift für Malakozoologie 7(5): 65–80 (July 1850), 7(6): 81–89 (August 1850).

Pfeiffer L (1853) Die Gattungen *Bulimus*, *Partula*, *Achatinella*, *Achatina* und *Azeca*. In Abbildungen nach der Natur mit Beschreibungen. In: Systematisches Conchylien-Cabinet von Martini und Chemnitz, Ersten Bandes, dreizehnte Abtheilung, erster Theil. (1) 13(1, Livraison 124): III–XIX, 65–96, pls. 19–24. Bauer & Raspe, Nürnberg.

Phung C-C, Yu FTY, Liew T-S (2017) A checklist of land snails from the west coast islands of Sabah, Borneo (Mollusca, Gastropoda). ZooKeys 673: 49–104. https://doi.org/10.3897/zookeys.673.12422

Pilsbry HA (1906a) Achatinidae: Stenogyrinae and Coeliaxinae. In: Tryon GW, Pilsbry HA. Manual of Conchology, Second Series: Pulmonata 18(70): 65–160[, pls. 11–20]. [Academy of Natural Sciences of Philadelphia, Philadelphia]

Pilsbry HA (1906b) Achatinidae: Stenogyrinae and Coeliaxinae. In: Tryon GW, Pilsbry HA. Manual of Conchology, Second Series: Pulmonata 18(71): 161–262[, pls. 21–34]. [Academy of Natural Sciences of Philadelphia, Philadelphia]

Pilsbry HA (1907) Achatinidae: Stenogyrinae and Coeliaxinae. In: Tryon GW, Pilsbry HA. Manual of Conchology, Second Series: Pulmonata 18(72): 273–357[, i–xii, pls. 35–51]. [Academy of Natural Sciences of Philadelphia, Philadelphia]

Pilsbry HA (1908) Caecilioides, Glessula and Partulidae. In: Tryon GW, Pilsbry HA. Manual of Conchology, Second Series: Pulmonata 20(77): 1–64[, pls. 1–10]. [Academy of Natural Sciences of Philadelphia, Philadelphia]

Pilsbry HA (1910) On *Opeas goodalli* Miller. The Nautilus 24: 31–32.

Pilsbry HA (1946) Land Mollusca of North America (North of Mexico). Vol. II. Part 1. The Academy of Natural Sciences of Philadelphia Monographs 3, 520 pp.

Pilsbry HA, Hirase Y (1904) Descriptions of new land shells of the Japanese Empire. Proceedings. Academy of Natural Sciences of Philadelphia 56: 616–638.

Potiez VLV, Michaud ALG (1838) Galerie des mollusques, ou catalogue méthodique, descriptif et raisonné des mollusques et coquilles du Muséum de Douai. Tome 1, xxxvi + 560 + 4 pp (Relevé des genres manquants; Errata). Atlas, 56 pp, 37 pls. Baillière, Paris.

Preece RC, Naggs F (2014) *Kaliella barrakporensis* (Pfeiffer), a new hot-house alien in Britain. Journal of Conchology 41(6): 781–782.

Preece RC, White TS, Raheem DC, Ketchum H, Ablett J, Taylor H, Webb K, Naggs F (2022) William Benson and the golden age of malacology in British India: Biography, illustrated catalogue and evaluation of his molluscan types. Tropical Natural History (Supplement 6): 1–434.

Probst J-M (2001) Description de quelques taxons de la faune malacologique introduite de La Réunion. Bulletin Phaethon 13: 1–3.

Raheem DC, Taylor H, Ablett J, Preece RC, Aravind NA, Naggs F (2014) A systematic revision of the land snails of the Western Ghats of India. Tropical Natural History (Supplement 4): 1–298.

Ranawana KB (2006) Land snails in Sri Lanka. In: Bambaradeniya CNB (Ed.) The fauna of Sri Lanka: status of taxonomy, research and conservation. The World Conservation Union, Colombo, Sri Lanka & Government of Sri Lanka, 84–99.

Rang S (1831) Description des coquilles terrestres recueillies pendant un voyage à la côte occidentale d’Afrique, et au Brésil. Annales des Sciences Naturelles 24(93): 5–63[, pls. 1–3].

Reischütz A, Reischütz PL, Richling I, Gilli C (2018) Die Molluskenfauna des Botanischen Gartens der Universität Wien. 2: Die Mollusken der Glashäuser. Nachrichtenblatt der Ersten Vorarlberger Malakologischen Gesellschaft 25: 31–41.

Richling I, von Proschwitz T (2021) Identification problems of travelling snail species—New exotic introductions to tropical greenhouses in Gothenburg, Sweden (Gastropoda: Achatinellidae, Strobilopsidae, Helicarionidae). PeerJ 9: e11185. https://doi.org/10.7717/peerj.11185

Robba E, Di Geronimo I, Chaimanee N, Negri MP, Sanfilippo R (2007) Holocene and Recent shallow soft-bottom mollusks from the Western Gulf of Thailand: Park Phanang Bay and additions to Phetchaburi fauna. Bollettino Malacologico 43(numero speciale): 1–98.

Robinson DG (1999) Alien invasions: The effects of the global economy on non-marine gastropod introductions into the United States. Malacologia 41: 413–438.

Robinson DG, Hovestadt A, Fields A, Breure ASH (2009) The land Mollusca of Dominica, Lesser Antilles. Zoologische Mededelingen Leiden 83: 615–650.

Rosenberg G, Muratov IV (2006) Status report on the terrestrial Mollusca of Jamaica. Proceedings. Academy of Natural Sciences of Philadelphia 155(1): 117–161. https://doi.org/10.1635/i0097-3157-155-1-117.1

Rowson B (2007) Land molluscs of Zanzibar Island (Unguja), Tanzania, including a new species of *Gulella* (Pulmonata: Streptaxidae). Journal of Conchology 39(4): 425–466.

Rowson B, Warren BH, Ngereza CF (2010) Terrestrial molluscs of Pemba Island, Zanzibar, Tanzania, and its status as an “oceanic” island. ZooKeys 70: 1–39. https://doi.org/10.3897/zookeys.70.762

Rumi A, Sánchez J, Ferrando NS (2010) *Theba pisana* (Müller, 1774) (Gastropoda, Helicidae) and other alien land molluscs species in Argentina. Biological Invasions 12: 2985–2990. https://doi.org/10.1007/s10530-010-9715-x

Rundell RJ (2010) Diversity and conservation of the land snail fauna of the western Pacific islands of Belau (Republic of Palau, Oceania). American Malacological Bulletin 28(1–2): 81–90. https://doi.org/10.4003/006.028.0223

Rutherford MG (2011) Land Snails from the Five-Islands Archipelago, North-west Trinidad, West Indies. Living World, Journal of The Trinidad and Tobago Field Naturalists’. Club 2011: 42–45.

Schileyko AA (1999) Treatise on terrestrial pulmonate mollusks. Part 4. Draparnaudiidae, Caryodidae, Macrocyclidae, Acavidae, Clavatoridae, Dorcasiidae, Sculptariidae, Corillidae, Plectopylidae, Megalobulimidae, Strophocheilidae, Cerionidae, Achatinidae, Subulinidae, Glessulidae, Micractaeonidae, Ferrussaciidae. Ruthenica (Supplement 2): 453–564.

Schileyko AA (2011) Check-list of land pulmonate molluscs of Vietnam (Gastropoda: Stylommatophora). Ruthenica 21(1): 1–68.

Schilthuizen M, Rutjes HA (2001) Land snail diversity in a square kilometre of tropical rainforest in Sabah, Malaysian Borneo. The Journal of Molluscan Studies 67(4): 417–423. https://doi.org/10.1093/mollus/67.4.417

Schmacker B, Boettger O (1891) Neue Materialien zur Charakteristik und geographischen Verbreitung chinesischer und japanischer Binnenmollusken II. Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft 23(9/10): 145–176, (11/12): 177–194.

Seebens H, Blackburn T, Dyer E, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, van Kleunen M, Winter M, Ansong M, Arianoutsou M, Bacher S, Blasius B, Brockerhoff EG, Brundu G, Capinha C, Causton CE, Celesti-Grapow L, Dawson W, Dullinger S, Economo EP, Fuentes N, Guénard B, Jäger H, Kartesz J, Kenis M, Kühn I, Lenzner B, Liebhold AM, Mosena A, Moser D, Nentwig W, Nishino M, Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE, Scalera R, Schindler S, Štajerová K, Tokarska-Guzik B, Walker K, Ward DF, Yamanaka T, Essl F (2017) No saturation in the accumulation of alien species worldwide. Nature Communications 8(1): 14435. https://doi.org/10.1038/ncomms14435

Shea M (2007) Exotic snails and slugs found in Australia. Malacological Society of Australasia Newsletter 131: 3–11.

Simone LRL (2006) Land and freshwater molluscs of Brazil. EGB, São Paulo, 390 pp.

Smith EA (1892) Of the land snails of St. Helena. Proceedings of the Zoological Society of London 1892: 258–270[, pls 21–22].

Smith EA (1895) Report on the land and fresh-water shells collected by Mr. Herbert H. Smith at St. Vincent, Grenada, and other neighbouring islands. Proceedings of the Malacological Society of London 1(1): 300–322.

Smith BJ (1989) Travelling snails. Journal of Medical and Applied Malacology 1: 195–204.

Smith BJ (1992) Non-marine Mollusca. Zoological catalogue of Australia, 8. Australian Government Publishing Service (AGPS), Canberra, Australia, [xi +] 399 pp.

Solem A (1964) New records of New Caledonian nonmarine mollusks and an analysis of the introduced mollusks. Pacific Science 18(2): 130–137.

Solem A (1989) Non-camaenid land snails of the Kimberley and Northern Territory, Australia, I. Systematics, affinities and ranges. Invertebrate Systematics 2(4): 455–604. https://doi.org/10.1071/IT9880455

Stanisic J, Cameron RAD, Pokryszko BM, Nekola JC (2007) Forest snail faunas from S.E. Queensland and N.E. New South Wales (Australia): Patterns of local and regional richness and differentiation. Malacologia 49(2): 445–462. https://doi.org/10.4002/0076-2997-49.2.445

Stanisic J, Shea M, Potter D, Griffiths O (2010) Australian land snails volume 1. A field guide to eastern Australian species. Mauritius, Bioculture Press for the Australian Museum, 591 pp.

Swainson W (1840) A treatise on malacology; or the natural classification of shells and shell-fish. Longman, London, [viii +] 419 pp. https://doi.org/10.5962/bhl.title.8027

Szczepkowski A, Gierczyk B, Kujawa A (2014) Greenhouses of botanical gardens as a habitat of alien and native macrofungi: A case study in Poland. Central European Journal of Biology 9: 777–795. https://doi.org/10.2478/s11535-014-0310-5

Tan SK, Lim KKP, Chua MAH (2015) Terrestrial snails and slugs (Mollusca: Gastropoda) of Pulau Tekong, Singapore. Nature in Singapore 8: 25–30.

Teodorescu I, Matei A (2010) Native and alien arthropods in several greenhouses (Bucharest area). Romanian Journal of Biology. Zoology 55(1): 31–42.

Thompson FG (2011) An annotated checklist and bibliography of the land and freshwater snails of Mexico and Central America. Bulletin of the Florida State Museum Biological Sciences 50(1): 1–299. https://doi.org/10.58782/flmnh.bnej7351

van Benthem Jutting WSS (1964) Non-marine Mollusca of West New Guinea. Part 3, Pulmonata, 1. Nova Guinea (Zoology) 26: 1–74.

van Bruggen AC (1981) *Cochlicopa lubricella* and *Helix aspersa* as alien land snails (Gastropoda, Pulmonata) in Zimbabwe/Rhodesia. Basteria 45: 71–72.

van Bruggen AC (2008) New studies on the land molluscs of Malawi, a second interim progress report. Prolegomena for a new checklist. Basteria 72: 353–368.

van Bruggen AC, van Goethem JL (2001) Prolegomena for a checklist of the terrestrial molluscs of the Upemba National Park, D.R. Congo. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique Biolologie 71: 151–168.

van Regteren Altena CO (1975) Land Gastropoda of Suriname, with the description of a new species of *Nesopupa*. Basteria 39(3/6): 29–50.

Verdcourt B (1983) A list of the non-marine Mollusca of East Africa (Kenya, Uganda, Tanzania, excluding Lake Malawi). Achatina 11: 200–239.

Verdcourt B (1986) The identity of some species of *Cecilioides* Férussac, 1814 from a river drift in Kenya (Mollusca, Ferussaciidae). Revue de Zoologie Africaine 99: 365–368.

Verdcourt B (2000) Molluscs. In: Burgess ND, Clarke GP (Eds) Coastal Forests of Eastern Africa. IUCN, Gland, Switzerland, 219–224. https://doi.org/10.1111/j.1095-8312.1998.tb00337.x

Verdcourt B (2006) A revised list of the non-marine mollusca of East Africa (Kenya, Tanzania and Uganda, excluding Lake Malawi). B Verdcourt, Maidenhead, UK, 75 pp.

Vermeulen JJ, Whitten AJ (1998) Fauna Malesiana guide to the land snails of Bali. Backhuys Publishers, Leiden, 164 pp.

Virgillito M, Miquel SE (2013) New records of exotic land snails and slugs in Argentina. Revista del Museo Argentino de Ciencias Naturales 15(2): 295–303. https://doi.org/10.22179/REVMACN.15.186

von Möllendorff OF (1890) Die Landschnecken-Fauna der Insel Cebu. Bericht über die Senckenbergische Naturforschende Gesellschaft in Frankfurt-am-Main (1890): 189–292[, pls 7–9]. https://doi.org/10.5962/bhl.title.13047

von Proschwitz T (1994) *Lamellaxis clavulinus* (Potiez & Michaud) as a greenhouse species in Sweden. Journal of Conchology 35(2): 184–185.

von Proschwitz T (2004) *Afropunctum seminium* (Morelet) as a green house species in Sweden. Journal of Conchology 38: 175–176.

von Proschwitz T (2016) Faunistical news from the Göteborg Natural History Museum 2015 – snails, slugs and mussels – with some notes on *Leptinaria unilamellata* (d'Orbigny) – a land snail species new to Sweden. Göteborgs Naturhistoriska Museum Årstryck 2016: 33–51.

Wang C, Zhang X, Pan X, Li Z, Zhu S (2015) Greenhouses: Hotspots in the invasive network for alien species. Biodiversity and Conservation 24(7): 1825–1829. https://doi.org/10.1007/s10531-015-0876-x

Wiegmann F (1894) Beiträge zur Anatomie der Landschnecken des Indischen Archipels. Zoologische Ergebnisse einer Reise in Niederländisch Ost-Indien 3: 112–259.

Wiktor A (2003) Terrestrial gastropods (Mollusca) of province Madang in Papua - New Guinea. Part III. Pulmonata: Rathousiidae, Ellobiidae, Succineidae, Agriolimacidae, Endodontidae (Partim), Ariophantidae, Euconulidae, Subulinidae, Streptaxidae. Folia Malacologica 11(1–2): 1–21. https://doi.org/10.12657/folmal.011.001

Wollaston TV (1878) Testacea Atlantica: Or the Land and Freshwater Shells of the Azores, Madeiras, Salvages, Canaries, Cape Verdes, and Saint Helena. L. Reeve & Company, [xi +] 588 pp. https://doi.org/10.5962/bhl.title.10705

Wu SP, Hwang CC, Huang HM, Chang HW, Lin YS, Lee PF (2007) Land molluscan fauna of the Dongsha Island with twenty new recorded species. Taiwania 52(2): 145–151.

ZooKeys 1208: 133–163 (2024)
DOI: 10.3897/zookeys.1208.24495

Research Article

New species and a fascinating diversity of Chironomidae (Diptera, Insecta) in and around an overlooked urban vernal pool

Armin Namayandeh[1,2], Sergio Guerra[2], Natasha Islam[2], Taylor James[2], Patrick L. Hudson[3], Edris Ghaderi[4,5], Thameena Yusuf[2], Adrian A. Vasquez[6], Jeffrey L. Ram[7]

1 *Department of Environmental and Life Sciences, Trent University, 1600 West Bank Drive, Peterborough, ON, Canada*
2 *Department of Physiology, School of Medicine, Wayne State University, Detroit, MI 48201, USA*
3 *5597 New Meadow Drive, Ypsilanti, MI 48197, USA*
4 *Department of Fisheries Sciences, Faculty of Natural Resources, University of Kurdistan, Sanandaj, Iran*
5 *Department of Fisheries and Aquatic Ecology, Faculty of Fisheries and Environmental Sciences, Gorgan University of Agricultural Sciences and Natural Resources, Gorgan, Iran*
6 *Department of Biology, College of Liberal Arts and Sciences, Mercer University, 1501 Mercer University Drive, Macon, GA 31207, USA*
7 *Department of Physiology, School of Medicine, Wayne State University, Detroit, MI 48201, USA*
Corresponding author: Armin Namayandeh (a.namayan@taxanama.org)

Abstract

In this study, the biodiversity of Chironomidae was investigated in Palmer Park Pond A, an urban vernal pond in Detroit, Michigan, USA. This study is developed as part of our ongoing Public Environmental Outreach Program at the Detroit Exploration and Nature Center in Palmer Park. Twenty-one Chironomidae species were discovered in and on the adjacent riparian vegetation of this pond using molecular and morphological methods. Three species *Bryophaenocladius palmerparcum* Namayandeh & Hudson **sp. nov.**, *Limnophyes stagnum* Namayandeh, Guerra & Ram **sp. nov.**, and *Rheocricotopus* (*s. s.*) *angustus* Namayandeh & Hudson **sp. nov.** are new to science. *Bryophaenocladius palmerparcum* **sp. nov.** and *L. stagnum* **sp. nov.** are unusual Orthoclads, with *B. palmerparcum* **sp. nov.** possessing a setose, short, and wide anal point and *L. stagnum* **sp. nov.** lacking lanceolate setae on both sexes. Based on the shape of superior volsella, *R. angustus* **sp. nov.**, belongs to the *effusus* group, which was also confirmed by DNA barcoding molecular analysis. In this study, a new faunistic record was also found for the Nearctic as well as four new faunistic records for the state of Michigan. Ephemeral aquatic habitats such as vernal pools are often overlooked or destroyed by urbanization activities, controlling vector species, creating groomed fields, and/or residential development. Therefore, finding these new species demonstrates the biodiversity value of vernal ponds as important habitats, further motivating us to preserve them.

Key words: *Bryophaenocladius*, Detroit, educational outreach, faunistic records, *Limnophyes*, *Rheocricotopus*, temporary aquatic habitats, urban park

Academic editor: Viktor Baranov
Received: 1 April 2024
Accepted: 11 June 2024
Published: 29 July 2024

ZooBank: https://zoobank.org/FFB06B11-084A-4C08-A050-AFBA7655DF2F

Citation: Namayandeh A, Guerra S, Islam N, James T, Hudson PL, Ghaderi E, Yusuf T, Vasquez AA, Ram JL (2024) New species and a fascinating diversity of Chironomidae (Diptera, Insecta) in and around an overlooked urban vernal pool. ZooKeys 1208: 133–163. https://doi.org/10.3897/zookeys.1208.24495

Introduction

Vernal pools are small, shallow, isolated bodies of water occurring ephemerally in or in relation to the woodlands that surround them. Their hydrologic regime is driven by the seasonality of precipitation (Colburn 2004), the surrounding land surface's relief and drainage characteristics, and the surrounding vegetation's evapotranspiration (Cartwright et al. 2022). Despite their ephemeral and isolated nature, they display a remarkable and distinct biodiversity of fauna, especially invertebrates. Among invertebrates, aquatic insects, particularly Chironomidae species, are an ever-present feature of these habitats. A long-term study of Sunfish Pond, a vernal pond in southern Ontario, produced some 98 invertebrate taxa, with Chironomidae present in almost all hydrologic phases of the pond (Williams 2006). A species of *Einfeldia* occurred during the entire aquatic phase of the ponds. Other species occurred during the first few days of spring, such as those in *Trissocladius*, *Eukiefferiella*, *Phaenopsectra*, *Parachironomus*, and *Polypedilum*. Some species appeared within the first few weeks of the pond formation, such as the species of *Micropsectra*, *Corynoneura*, *Ablabesmyia*, and *Psectrotanypus*, and others appeared before ponds dried up, such as the species of *Cricotopus*. Williams (2006) reported no Chironomidae during the drought cycle of Sunfish Pond. However, we know from other studies that many species of Chironomidae can resist the drought in temporary habitats either by cryptobiosis, diapause, cocoon forming, or by migrating to the deeper part of the substrate or hyporheic zone (Hinton 1960; Jones 1975; Grodhaus 1976; Delettre 1986; McLachlan 1988; Frouz et al. 2003; Suemoto et al. 2004; Cornette et al. 2022).

Temporary habitats such as vernal pools are often overlooked, as the value of biodiversity conservation is usually prioritized for exotic places (DeGasparro et al. 2020). Many times, new faunistic records and biogeographical gaps in species distribution can be filled by studying overlooked habitats, especially in places regarded as disturbed, such as farms and natural habitats of urban areas (Owen and Owen 1975; Quistberg et al. 2016; Namayandeh and Beresford 2017; DeGasparro et al. 2020; Griffiths-Lee et al. 2022). An advantage of urban natural habitats is that scientists can engage and motivate the public in the collection of specimens occurring closer to home (Dearborn and Kark 2010). Furthermore, researchers can provide environmental education to people with no background or specialization, such as high school and undergraduate students. The ecological importance of temporary habitats can be seen by emphasis on their value as refugia or connecting habitat patches with metacommunities and metapopulations. In this mosaic of connecting habitats, the disturbance rate (e.g., drought) can determine the expansion or reduction of species populations. However, local extinction does not necessarily cause the regional population to be exterminated (Larned et al. 2010).

We developed this study as part of our ongoing Public Environmental Outreach Program at Detroit Exploration and Nature Center (DEN), located at the northern edge of Palmer Park, Detroit, Michigan. We also engaged and trained four premed students from Wayne State University to perform DNA extractions, amplification, sequence analysis, and PCR as part of our educational outreach goals. The study area, Palmer Park, is a 200-hectare managed urban park that contains a primary (i.e., virgin) forest. The area surrounding Palmer Park is a typical built-up urban environment. Within the woods, there are many naturally occurring vernal ponds. One, in particular, is a sizeable vernal pool that we have monitored for nearly two years, during 2022–2023, named Palmer Park Pond A, referred to hereafter as Pond A.

Despite its ephemeral nature, we collected 20 Chironomidae species in and around (i.e., riparian zone) this overlooked urban habitat. Three species, *Bryophaenocladius palmerparcum* sp. nov., *Limnophyes stagnum* sp. nov., and *Rheocricotopus* (*s. s.*) *angustus* sp. nov. are new to science. Additionally, we report one new faunistic record for the Nearctic and four new faunistic records for Michigan. We also found and described the adult male of a morphospecies, likely to be the *Chironomus* sp. *parariparius* described by Martin (2023). These records further improve the existing biogeographical gaps for the distribution of Chironomidae species in the Nearctic and the Holarctic.

Materials and methods

Study area

Vernal Pond A is located in Witherell Woods, 90 acres of virgin forest in Palmer Park, elevation ca 190 m, 42.42766°N, 83.11741°W. Based on the visual observation of the water level displayed in a hydrograph obtained from the pond, 2022–23, the pond's wet phase (i.e., period) of the pond starts in mid to late winter, March or early April, and could last until late June. However, depending on winter and spring precipitation, the pond could dry up as early as late May or early June. The dry phase starts mid-summer and lasts until early winter, January, or February (Figs 1, 2A–D).

Sampling collection, preparation imagery, and faunistic records

We collected the aquatic larvae and the emerging adults from and around Pond A. Larvae were collected using a hand-held net and kicking the substrate for 3 minutes in random habitats in the pond. The net contents were emptied and thoroughly washed into a 6 mm mesh-size sieve mounted on a 250-μm mesh sieve. We emptied the content of the 250-μm sieve into a 473-ml bottle and placed samples in an ice chest for transport to the lab for sorting within one to two days. For longer-term preservation, 90% ethanol was added to the collected organisms. Adults were collected with a self-built emergence similar to the design of Cadmus et al. (2016) and by sweep net from the vegetation around the pond's edges preserved in 90% ethanol (Fig. 2E, F). We sorted the adults

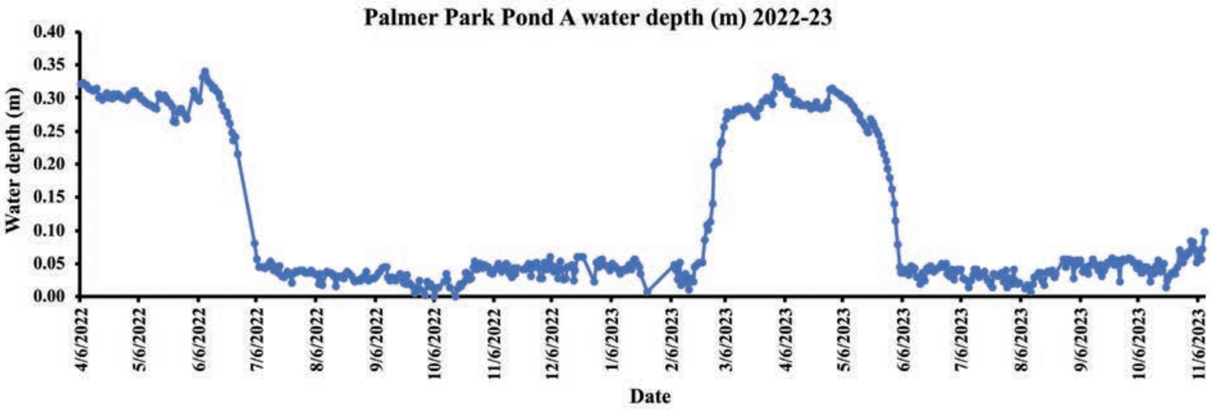


Figure 1. A hydrograph of Palmer Park Pond A water depth (m) 2022–23.

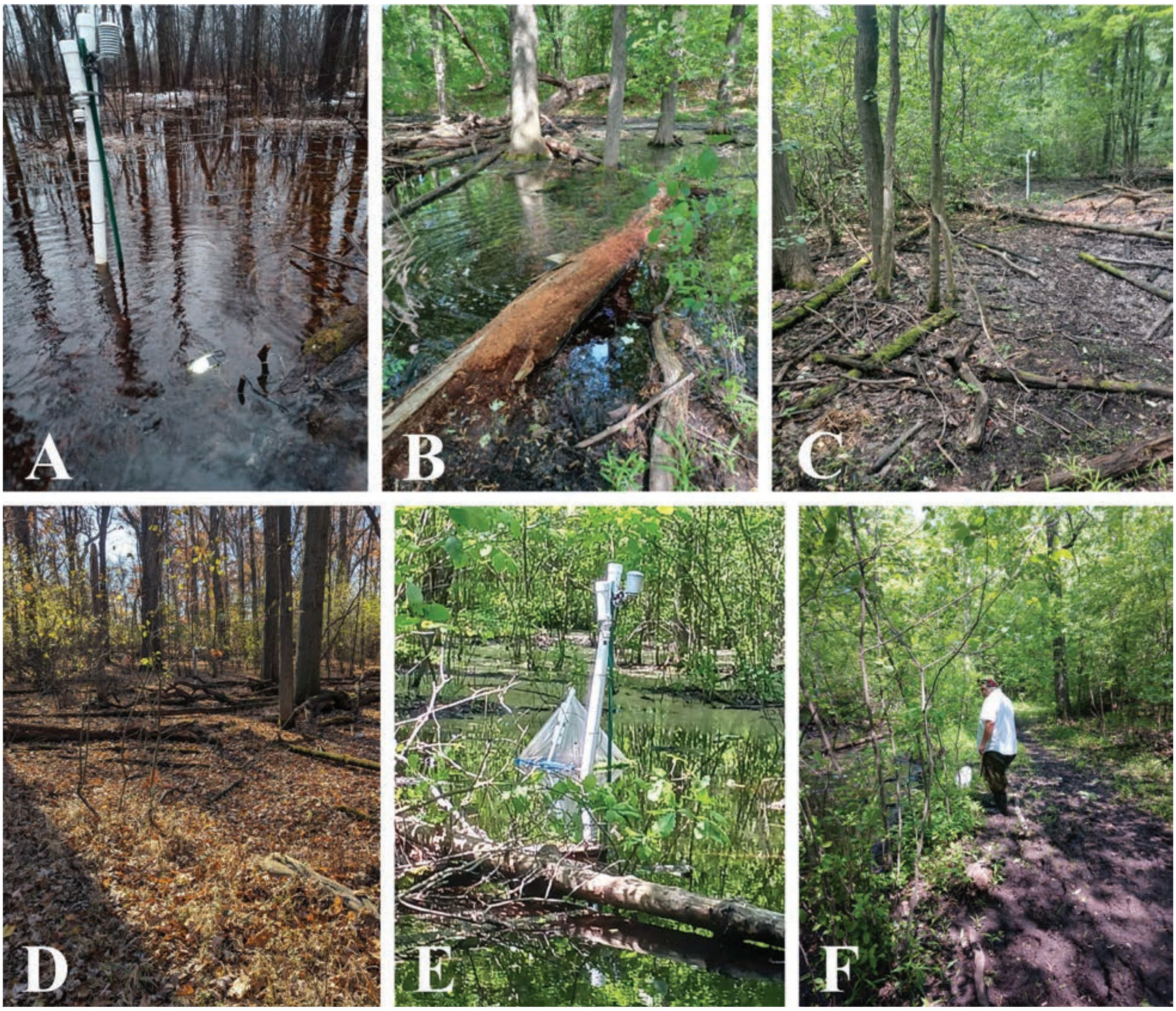


Figure 2. The study habitat, Palmer Park Pond A, Detroit, Michigan, USA **A** wet phase in late March **B** wet phase in late May **C** dry phase in late June **D** dry phase in November **E** emergence trap **F** collecting adults using sweep nets on riparian vegetation.

and immatures using a sorting scope and mounted them using a procedure outlined in Namayandeh and Hudson (2022). The depth of the pond was measured using a Dragino LDDS20 LoRaWAN Liquid Level Sensor, installed in the deepest part of the pond. The depth was measured from the water surface to the sensor, which was very close to the pond's substrate. We corrected the values that were considered noise in the data, defined as data obtained due to the instrument's temporary malfunction, for instance, temporary blockage by leaf litter, sediment, or invertebrates.

The imagery was produced using a Diagnostic Instruments Inc. Spot 5.1 camera mounted on an Olympus BX51 compound scope. The illustrations were produced based on the obtained images using Inkscape 1.2.2(2022): Draw Freely software. Morphological terminology, abbreviation, and measurements follow those of Sæther (1977, 1980).

The locations and depositories of species are as follows: Michigan State University, the Albert J. Cook Arthropod Research Collection (**ARC**); Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Canada

(**CNC**); Centre for Biodiversity Genomics, University of Guelph, Canada (**CBG**); private collection of Patrick L. Hudson, Ypsilanti, Michigan, USA (**PLH**); private collection of Thomas Bendt, Heyerhütte, Germany (**TB**).

We determined the new records by examining all available catalogs, such as those of Ashe and O'Connor (2012), Bright (2024), Caldwell et al. (1997), Cranston and Oliver (1988), and Oliver et al. (1990). Additionally, based on the DNA sequences we obtained in this study, we examined all matching sequences in BOLD and GenBank and their corresponding geographical location.

Molecular and phylogenetic analyses

We could only extract sufficient DNA for amplification and successful sequencing from ten of 20 species in this study. The condition of the tissues and scarcity of specimens prevented us from either extracting DNA or dedicating the whole animal tissue to the molecular barcoding procedure described below. Genomic DNA was extracted from the full tissues of the adults and larval Chironomidae using the Qiagen DNA Blood and Tissue Kit (Qiagen, Inc., Germantown, MD) as described previously by Failla et al. (2016) and Vasquez et al. (2022). A 658 base pair fragment of the cytochrome oxidase subunit 1 (COI) was amplified using the universal primers LCO1490 and HCO2198 (Folmer et al. 1994). DNA amplification was carried out in 20 µl reactions using GoTaq DNA polymerase (Promega Co., Madison, WI), 1× manufacturer's buffer, 10 mM dNTP mix, 10 mM of each primer, and 200–250 ng template DNA. The amplification cycles were performed using an initial denaturation step of 95 °C for five min, followed by 34 cycles of 94 °C for 30 s, 51 °C for 30 s, 72 °C for one min, and a final extension at 72 °C for three min. The amplicons were shipped to GENEWIZ, a subsidiary of Azenta Life Sciences, for Sanger Sequencing. Sequence traces were evaluated and edited with Chromas 2024 (http://www.technelysium.com.au/chromas.html). We submitted new sequences to the BOLD database (http://dx.doi.org/10.5883/DS-DTPPA). The list of sequences, codes, GenBank, or BOLD accessions is provided in Suppl. material 1: table S1.

Phylogenetic trees based on COI sequences were created using Neighbour-Joining (NJ) and Maximum Likelihood (ML) methods. The NJ phylogenetic tree was made using Kimura's 2-parameter (K2P) model in MEGA X with 10000 bootstrap replications (Kumar et al. 2018). To construct the tree using ML, sequences were aligned using Clustal X v. 2.1 software (Larkin et al. 2007). The resulting alignment was analyzed in jModelTest software v. 2.1.7 (Darriba et al. 2012) to determine the optimal model of molecular evolution and gamma rate heterogeneity using the AIC. We constructed the ML trees using RAxML-HPC BlackBox (8.2.12) software (Stamatakis 2014) in the CIPRES Scientific Gateway v. 3.3 XSED (Miller et al. 2012) and with 10000 Bootstrap repeats. Trees constructed in the ML model were visualized in FigTree v. 1.4.2 (Rambaut 2014). *Culicoides sanguisuga* Gornostaeva, 1977, *Bryophaenocladius scanicus* (Brundin, 1947), and *Chironomus* (*s. s.*) *maturus* Johannsen, 1908 sequences obtained from BOLD were used as out group in phylogenetic trees. We obtained the phylogenetic distances using Kimura-2-parameter (K2P) model (Kimura 1980) in MEGA X (Kumar et al. 2018). We first determined the intraspecific K2P distance between the sequences from this study and the intraspecific K2P distance between sequences available in BOLD and NCBI.

To determine the limits of "molecular species" we used Automatic Barcode Gap Discovery (ABGD) (Puillandre et al. 2012). (https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html) and K2P distances, which we considered 5% as a threshold value. We ran ABGD with P min = 0.001, P max = 0.1, and a gap width of 1.5, all for a total of 10 steps setting to calculate the barcode gap in the distribution of pairwise differences.

Results

Molecular and phylogenetic analyses

The analyses of NJ and ML on sequences of Chironomidae from Pond A and those obtained from NCBI and BOLD produced different tree topologies, with NJ more appropriately separating the genera into appropriate subfamilies (Suppl. material 1: fig. S1). Based on the NJ analysis, *Chironomus* (*s. s.*) *acidophilus* Keyl, 1960, represented by a single sequence barcode clustered with two voucher sequences of *C. acidophilus*, accession numbers KR663763 and HQ581839, from Ontario, Canada (Hebert et al. 2016). The two sequences of *Chironomus* (*s. s.*) *maturus* Johannsen, 1908 from Pond A clustered with voucher sequences of *C. maturus*, accession numbers MF707093 and HQ581849, from Ontario, Canada (de Waard et al 2019). The single sequence of *Tanytarsus* we identified as *Tanytarsus guerlus* (Roback, 1957) clustered with two sequences of *T. guerlus*, accession numbers KR657911, and KR638783 from Ontario, Canada (Hebert et al. 2016). The two sequences of *Polypedilum* we identified as *Polypedilum* (*s. s.*) sp. clustered with sequences identified only as *Polypedilum* sp., accession numbers HQ982463 and HQ981830, from Ontario, Canada. The single sequence of *Smittia terrestris* from Pond A clustered with sequence of *Smittia* species accession number HQ582868, and *Smittia terrestris* (= *Bryophaenocladius terrestris*), accession number OP927437 from Rathenow-Grütz, Germany (Chimeno et al. 2023), and accession numbers HQ582868, HQ981435, from Arkansas, USA, and Ontario, Canada.

The average intraspecific K2P distance between the specimens of *C. maturus* was 0.002 (0.20%), for the specimens of *C. acidophilus* 0.001 (0.1%), for *T. guerlus* 0.001 (0.1%) and for *S. terrestris* 0.002 (0.2%). These results further confirm the new faunistic records for Michigan and the Nearctic. Kimura 2-Parameter (K2P) average interspecific distances for all Pond A species is provided in Suppl. material 1: table S3.

The analyses of NJ and ML on sequences of *Limnophyes* from Pond A and those obtained from NCBI and BOLD produced the same tree topology (Fig. 3). The six sequences of *L. stagnum* sp. nov., from Pond A, clustered with two sequences identified as *Limnophyes* sp., accession numbers MF727341 and CNTIC4604, from Ontario, Canada (Hebert et al. 2016, de Waard et al. 2019). The average intraspecific K2P distance calculated for the six sequences of *L. stagnum* sp. nov. and the two sequences of *Limnophyes* sp. from Ontario was 0.001 (0.1%). The average interspecific K2P distance of *L. stagnum* sp. nov., with other *Limnophyes* species was 0.17 (17%). The average interspecific K2P distance for all species of *Limnophyes* was 0.15 (15%) (Suppl. material 1: table S3).

The analyses of NJ and ML on sequences of *Rheocricotopus* from Pond A and those obtained from NCBI and BOLD produced slightly different tree

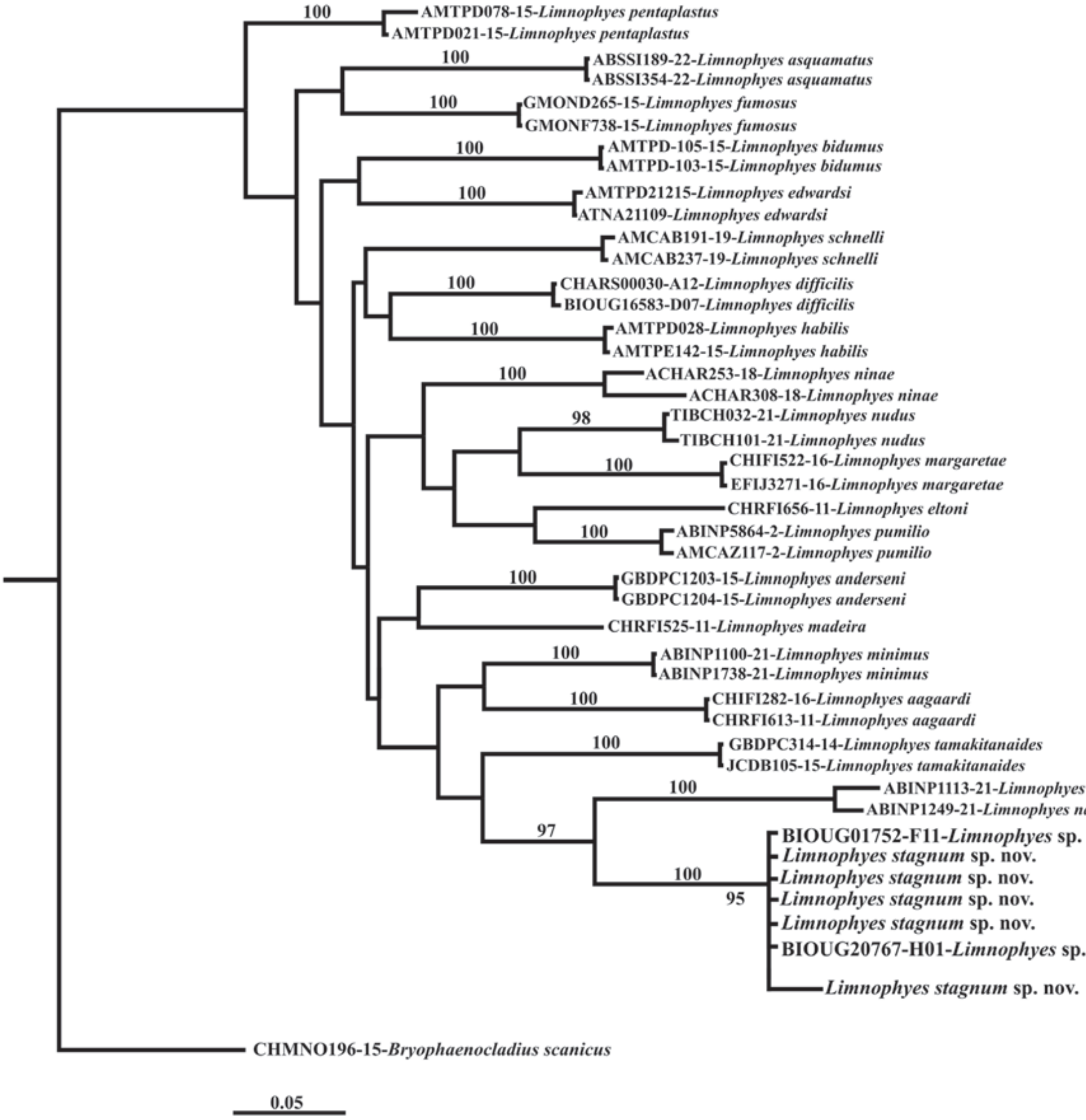


Figure 3. Neighbour-Joining (NJ) and Maximum Likelihood (ML) trees of *Limnophyes* Eaton, 1875 species, and one outgroup *Bryophaenocladius scanicus* (Brundin, 1947) inferred from the COI nucleotide sequence data (658 bp). Numbers on branches represent the bootstrap value for Neighbor-Joining (NJ) and Maximum Likelihood (10,000 replicates, with values < 95 omitted). Support numbers are equal in both methods.

topologies, with ML more appropriately demonstrating the relationship among species of *Rheocricotopus* (Fig. 4). The two sequences of *R. angustus* sp. nov., from Pond A, clustered with two sequences identified as *Rheocricotopus* sp., accession numbers KR474365.1 and KR470368.1, from Ontario and Yukon Territory, Canada (Hebert et al. 2016). The average intraspecific K2P distance calculated for the two sequences of *R. angustus* sp. nov. with the two sequences of *Rheocricotopus* sp. from Ontario and Yukon was 0.012 (1.2%). The average interspecific K2P distance of *R. angustus* sp. nov. with other *Rheocricotopus* species was 0.16 (16%). The average interspecific K2P distance for all species of *Rheocricotopus* was 0.15 (15%) (Suppl. material 1: tables S4).

Using ABGD, we saw a gap between the highest intraspecific K2P distance (0.05 or 5%) and the lowest interspecific K2P distance (0.11 or 11%) for

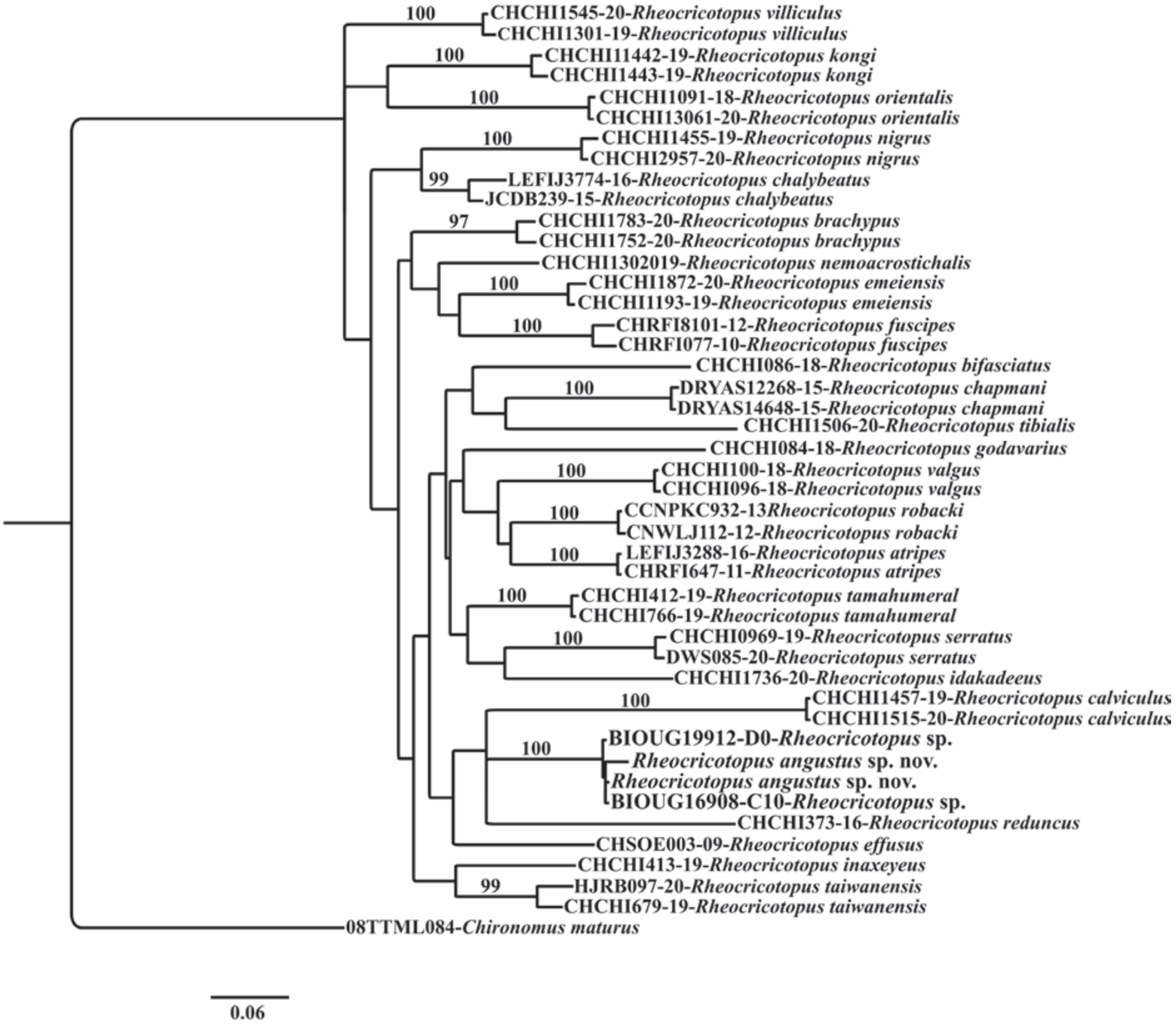


Figure 4. Neighbour-Joining (NJ) and Maximum Likelihood (ML) trees of *Rheocricotopus* Brundin, 1956 species, and one outgroup *Chironomus (s. s.) maturus* Johannsen, 1908 inferred from the COI nucleotide sequence data (658 bp). Numbers on branches represent the bootstrap value for Neighbor-Joining (NJ) and Maximum Likelihood (ML) (10,000 replicates, with values < 95 omitted). Support numbers are equal in both methods.

Limnophyes species. This gap (i.e., for sequences used) suggests that if the distance between two sequences is less than 5%, the sequences belong to the same species, and if it is more than 11%, the sequences belong to two different species. Using ABGD, we also saw a gap between the highest intraspecific K2P distance (0.04 or 4%) and the lowest interspecific K2P distance (0.09 or 9%) for *Rheocricotopus* species. The gaps of 6% and 5% obtained in this study, based on the distance-based methods of ABGD, support species independence (Fig. 5A, B).

Faunistic records

A total of 20 species of Chironomidae were found in Palmer Park Pond A (Fig. 6; Table 1). Three species *Bryophaenocladius palmerparcum* sp. nov., *Limnophyes stagnum* sp. nov., and *Rheocricotopus* (*s. s.*) *angustus* sp. nov.,

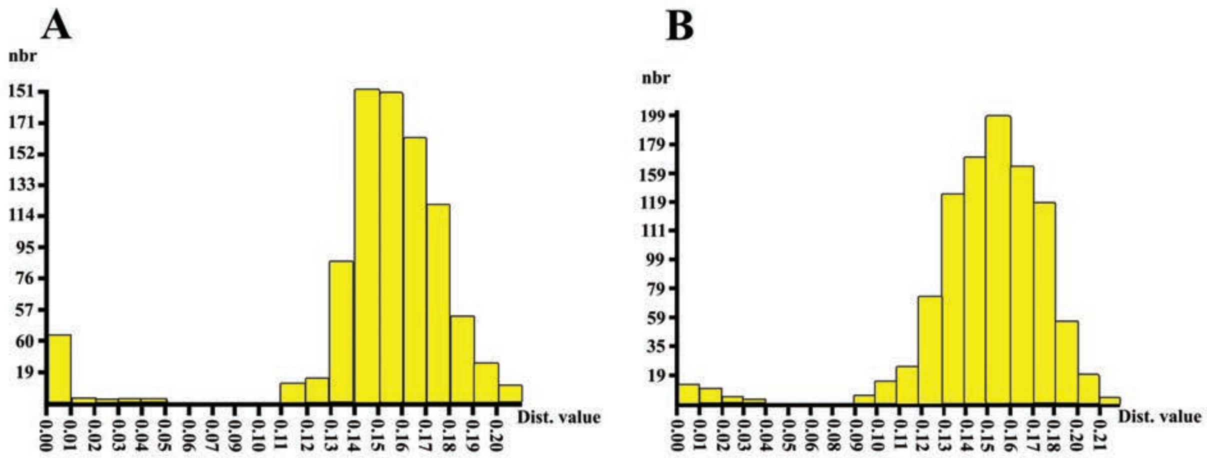


Figure 5. Histogram of genetic distance estimates from ABGD (Automatic Barcode Gap Discovery) for partition analyses **A** 48 cytochrome oxidase subunit1 sequences of the *Limnophyes* Eaton, 1875 species **B** 44 cytochrome oxidase subunit1 sequences of the *Rheocricotopus* Brundin, 1956. nbr = number of runs.

Table 1. List and life stages of species of Chironomidae collected from Palmer Park Pond A, 2022–23. M = Male, F = Female, P = Pupa, L = Larva, N = No, Y = Yes.

Species	Life stage	Barcoded
Labrundinia pilosella (Loew, 1866)	1M	N
Allocladius nanseni (Kieffer, 1926)	1M	N
Bryophaenocladius palmerparcum sp. nov.	3M	N
Cricotopus (*Isocladius*) *intersectus* (Staeger, 1839)	1F	N
Diplosmittia harrisoni Sæther, 1981	1M	N
Rheocricotopus (s. s.) angustus sp. nov.	3L	Y
Limnophyes stagnum sp. nov.	2M, 7F	Y
Smittia aterima (Meigen, 1818)	5M	Y
Smittia terrestris (Thienemann & Strenzke, 1941)	20F	Y
Chironomus (*s. s.*) *acidophilus* Keyl, 1960	4M	Y
Chironomus (*s. s.*) *bifurcatus* Wülker et al., 2009	1M	N
Chironomus sp. '*butleri*' by Martin, 2023	2M	Y
Chironomus (*s. s.*) *maturus* Johannsen, 1908	6M, 2F, 1P, 33L	Y
Chironomus (*s. s.*) *atrella* (Townes, 1945)	2M	Y
Chironomus (*Lobochironomus*) *dorsalis* Meigen, 1818	2M	N
Chironomus nr. sp. *parariparius* by Martin 2023	1M	N
Kiefferulus dux (Johannsen, 1905)	5M	N
Polypedilum (*s. s.*) sp.	10M	Y
Tanytarsus guerlus (Roback, 1957)	6M	Y
Tribelos jucundum (Walker, 1858)	4M	N

are new to science. *Polypedilum* (*s. s.*) sp. is possibly a new species. *Smittia terrestris* (Thienemann & Strenzke, 1941) is a new faunistic record for the Nearctic. *Chironomus* (*s. s.*) *acidophilus* Keyl, 1960, *Chironomus* (*s. s.*) *maturus* Johannsen, 1908, *Chironomus* (*Lobochironomus*) *dorsalis* Meigen, 1818, and *Tanytarsus guerlus* (Roback, 1957) are new faunistic records for Michigan.

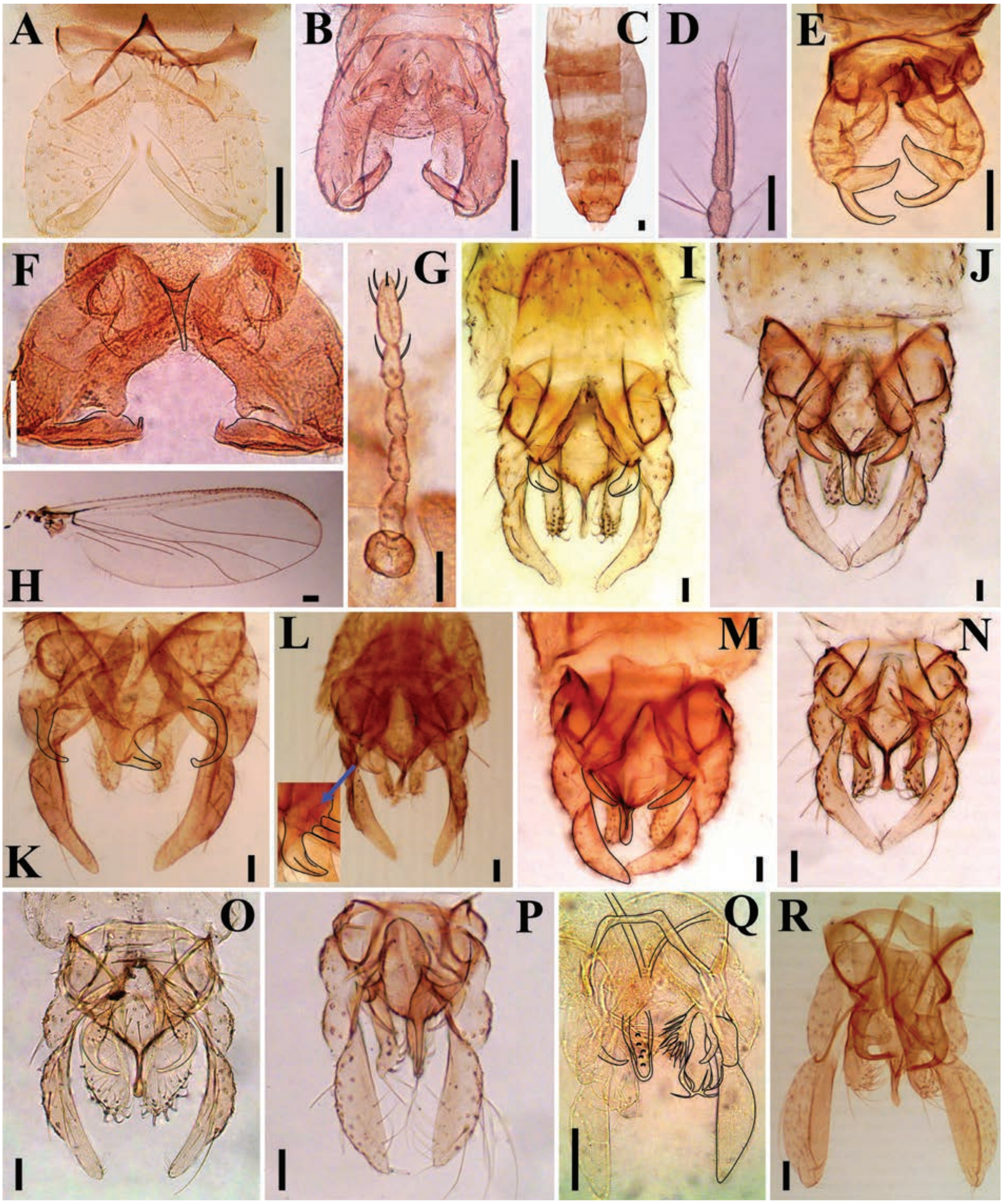


Figure 6. Gallery of Chironomidae species collected from Pond A, 2022–23 **A.** *Labrundinia pilosella* (Loew, 1866) **B** *Allocladius nanseni* (Kieffer, 1926) **C, D** *Cricotopus* (*Isocladius*) *intersectus* (Staeger, 1839) **E** *Diplosmittia harrisoni* Sæther, 1981 **F** *Smittia aterima* (Meigen, 1818) **G, H** *Smittia terrestris* Goetghebuer, 1941 **I** *Chironomus* (*s. s.*) *acidophilus* Keyl, 1960 **J** *Chironomus* (*s. s.*) *bifurcatus* Wülker et al., 2009 **K** *Chironomus* sp. '*butleri*' of Martin (2023) **L** *Chironomus* (*s. s.*) *maturus* Johannsen, 1908 **M** *Chironomus* (*s. s.*) *atrella* (Townes, 1945) **N** *Chironomus* (*Lobochironomus*) *dorsalis* Meigen, 1818 **O** *Kiefferulus dux* (Johannsen, 1905) **P** *Polypedilum* (*s. s.*) sp. **Q** *Tanytarsus guerlus* (Roback, 1957) **R** *Tribelos jucundum* (Walker, 1858). **, B, E, F, I–R** male hypopygium **C** female sternites and genitalia **D, G** female antenna **H** female wing. Scale bars: 50 µm.

Taxonomy

Subfamily Orthocladiinae

Bryophaenocladius palmerparcum **Namayandeh & Hudson sp. nov.**
https://zoobank.org/E9668141-118E-4C08-A504-A65A97E08615
Fig. 7A–D

Type material. ***Holotype*** 1 male; USA, Michigan, Detroit, Palmer Park, Pond A; 42.42766°N, 83.11741°W; leg. P.L. Hudson; 30.vi.2022, dep. ARC. ***Paratypes*** 2 males; same as holotype except leg. A. Namayandeh; 28.vi.2023, dep. ARC.

Diagnostic characters. The adult male of *B. palmerparcum* sp. nov. can be distinguished from other *Bryophaenocladius* Thienemann, 1934 males by the combination of the following characters: AR 1.4–1.5; costa not well-extended; anal point short, wide, and triangular, not surpassing the apex of tergite IX, with 11–15 setae; virga inconspicuous, consists of two long spines, looped; sternapodeme straight without large oral projections; superior volsella collar shaped; inferior volsella absent; gonostylus straight with a mid-section wide, and short collar-shaped crista dorsalis; HR 1.5–1.9; HV 2.6–2.9.

Description. Male (*n* = 3; unless otherwise stated). Total length 2.7–3.4 mm, Wing 1.4–1.7 mm long and 0.4 mm wide.

Coloration. Head, abdomen, and halter dark brown. Thorax dark brown with much paler yellowish areas in portion of dorsocentrals, in anteprontal, anepisternum, and apical portion of preepisternum regions. Legs golden brown. Wing greyish brown.

Head (Fig. 7A, B). Antenna with 13 flagellomere, last flagellomere with 10 sensilla chaetica, each of 2nd and 3rd flagellomere with pair of sensilla chaetica; shaft starts at base of 4th flagellomere (Fig. 7A); AR 1.4–1.5. Temporal setae 9, uniserial. Tentorium 150–190 µm long, tentorial pit close to apex. Clypeus squared, 101 µm long and 125 µm wide, with 20 setae, setae 73 µm long (*n* = 1). Palpal segments lengths (in µm): 55–77, 66; 33–57, 45; 157–164, 161; 125–131, 128; 93, third palpomere with 3 sensilla clavata, and without any projection.

Thorax (Fig. 7C): Achrostichals 8–10, starting close to antepronotum; dorsocentrals 12–23, 18 in two rows; prealars 4–6, 5; scutellars 12; antepronotals 3 basoventrally.

Wing (Fig. 7D): Brachiolum with 2 setae; R with 7–13, 10 setae; R_1 with 4 setae; R_{4+5} with 4 setae; other veins bare. Squama with 7–8 setae. Anal lobe produced and squared. Costa not well-extended, 17–20, 18 µm long. Microtrichia visible at 10 × magnification.

Legs. Foreleg spur 58 µm long (*n* = 1), midleg spur 30 µm long (*n* = 1), other spur damaged; hindleg spurs damaged, hind tarsus missing, hindleg comb with 12 spines (*n* = 1). Lengths and proportions of legs as in Table 2.

Table 2. Male leg lengths (µm) and proportions of *Bryophaenocladius palmerparcum* sp. nov.

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR	BV	SV
P_1	627	748	729	252	169	116	81	0.97	3.4	1.9
P_2	718	805	391	214	142	104	73	0.50	–	0.50
P_3	828	990	–	–	–	–	–	–	–	–

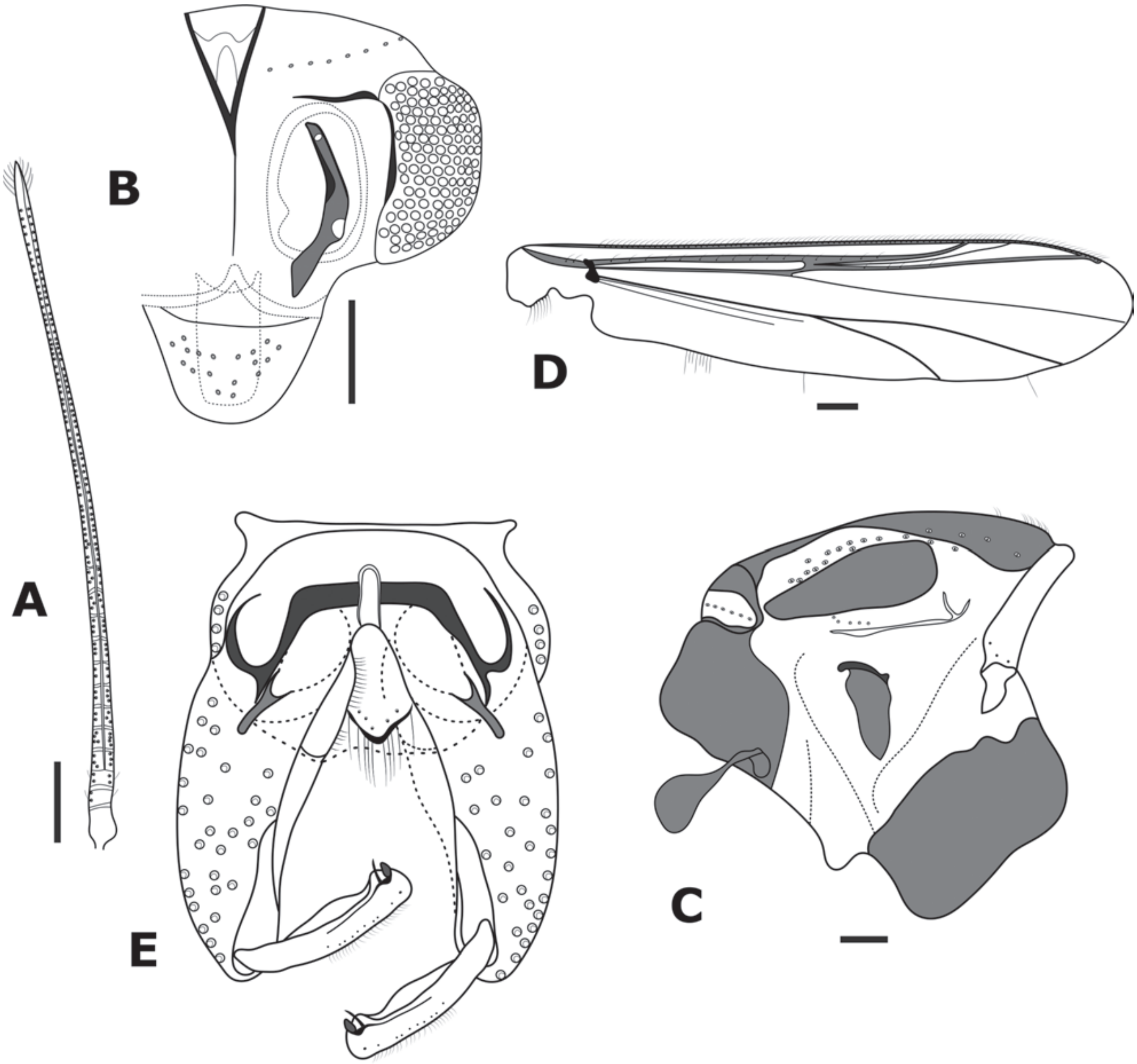


Figure 7. *Bryophaenocladius palmerparcum* sp. nov., adult male **A** antenna **B** head **C** thorax **D** wing **E** hypopygium. Scale bars: 100 μm.

Hypopygium (Fig. 7E): Anal point short, wide, and triangular, not surpassing the apex of tergite IX, 18 μm long and 34 μm wide at the base (*n* = 1), surface with 11–15, 12 setae. Virga inconspicuous, consists of two long spines, looped, 58 μm long (*n* = 1). Sternapodeme straight with large oral projections, 84–104, 97 μm long. Phallapodeme 42–50, 45 μm long. Superior volsella collar shaped, inferior volsella absent. Gonocoxite 158–216, 187 μm long. Gonostylus straight with a mid-section wide and short collar-shaped crista dorsalis, gonostylus 102–114, 110 μm long, megaseta 9 μm long. HR 1.5–1.9, 1.7; HV 2.6–2.9, 2.8.

Female and immatures. unknown.

Etymology. The species is named after the locality where it is found, Palmer Park. The word *parcum* is Latin, meaning park.

Distribution. USA (Michigan).

Remarks. A combination of strong decumbent achrostichals close to antepronotum; bare wing with strong punctation of microtrichia, and weak lateral spines attached to the shaft of hind and mid legs spines places this species in *Bryophaenocladius*. Although, in general, the long, prominent, and hyaline anal point defines many known species of *Bryophaenocladius*, the character of the short anal point of this species is not uncommon, and it has been observed among other known species of this genus. Previously, Donato et al. (2024) have demonstrated that the species of *Bryophaenocladius* show a significant pattern of anal point size and shape differences. For instance, among those species with short anal points, *Bryophaenocladius scleras* Wang, Liu & Epler, 2012 from the Nearctic has a short semicircular anal point (see Wang et al. 2004), and *Bryophaenocladius pleuralis* (Malloch, 1915) has a dark short anal point that does not extend beyond tergite IX (Makarchenko and Makarchenko 2009). Additionally, Epler (2012) described brachypterous *Bryophaenocladius chrissichuckorum* with a wide and short, triangular anal point similar to that of *B. palmerparcum* sp. nov. The first author has also observed this character of short anal point in Neotropical species (AN pers. obs. of specimens from Costa Rica). What is also observable is that besides the variation in shape and size of the anal point, as discussed in Donato et al. (2024), those species with the short anal point can still possess the hyaline section, such as *Bryophaenocladius inconstans* Brundin, 1947 and some lacking, such as the case of *B. palmerparcum*, *B. chrissichuckorum* and *B. pleuralis*. Therefore, the presence of an anterior hyaline section of the anal point can also separate species with a reduced anal point.

Limnophyes stagnum **Namayandeh, Guerra & Ram sp. nov.**

https://zoobank.org/38F6ED6F-9E46-4A00-93EE-0110BF969C6C
Figs 8, 9

Type material. ***Holotype*** 1 male; USA, Michigan, Detroit, Palmer Park, Pond A; 42.42766°N, 83.11741°W; leg. P.L. Hudson; 29.xi.2023, dep. ARC. ***Paratypes*** 2 males, 3 females; same as holotype.

Diagnostic characters. Adults of this species can be separated from other *Limnophyes* by the combination of the following characteristics: Adults with no thoracic lanceolate setae and 2 prescutellars; adult male without humeral setae, female with single humeral setae; male with 3 epimerons, 1 posterior anepisternum II, 1–2 preepisternals anteriorly parallel to antepronotum and close to anapleural suture; female with 2 posterior anepisternals II; 6 epimeron II; 11 preepisternals which 9 anteriorly clustered horizontally, separated from 2 vertical; male antenna with 10 flagellomeres and AR 0.86; female antenna with 4 flagellomere and AR 0.5; male anal point extremely short, almost receded, wide and triangular with apex rounded and gonostylus expanded evenly from base to apex; female with apodeme lobe not distinct; cercus pediform.

Description. Male (*n* = 3, unless otherwise indicated). Total length 1.8–1.9 mm. Wing 0.91–1.1 mm long and 0.3 mm wide.

Coloration. Head, thorax, legs, tergites, sternites, and hypopygium blackish brown. Wings and halters grey.

Head (Fig. 8A, B). Antenna with 10 flagellomeres, last flagellomere with 4 sensilla chaetica, groove starts at the apex of the second segment (Fig. 8A), AR 0.86 (*n* = 1). Eyes bare, without dorsomedial extension. Temporal setae 1 inner

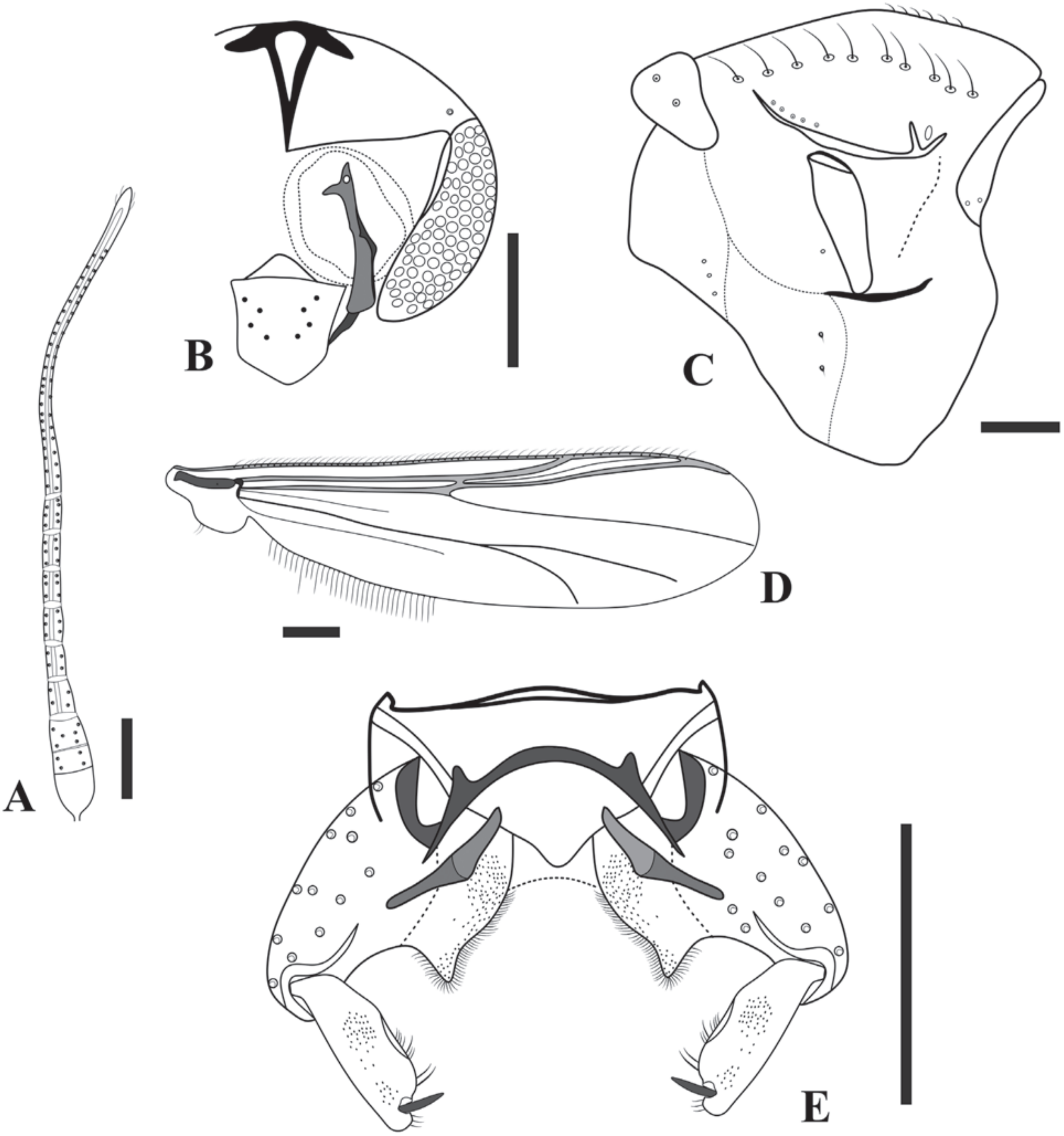


Figure 8. *Limnophyes stagnum* sp. nov., adult male **A** antenna **B** head **C** thorax **D** wing **E** hypopygium. Scale bars: 100 μm.

vertical (Fig. 8B). Tentorium 113–123, 118 μm long. Clypeus triangular, 82–95, 88 μm long and 106–125, 116 μm wide, bearing 8–10, 9 setae, setae 42–71, 56 μm long. Palpal segment lengths (in μm): 38, 36, 58, 54, 83 (*n* = 1).

Thorax (Fig. 8C). Lanceolate setae absent. Acrostichals 6; dorsocentrals 9–10; prealars 5; scutellars 4 in single row; antepronotals 2; lanceolate humerals absent; 2 prescutellars; epimeron 3; posterior anepisternum II 1; 1–2 preepisternals anteriorly parallel to antepronotum and close to anapleural suture.

Wing (Fig. 8D). Brachiolum with 1 seta. Squama with 2 setae. All veins bare. Costa extension 62 μm long (*n* = 1). Anal lobe well-reduced. Microtrichia visible at 10 ×.

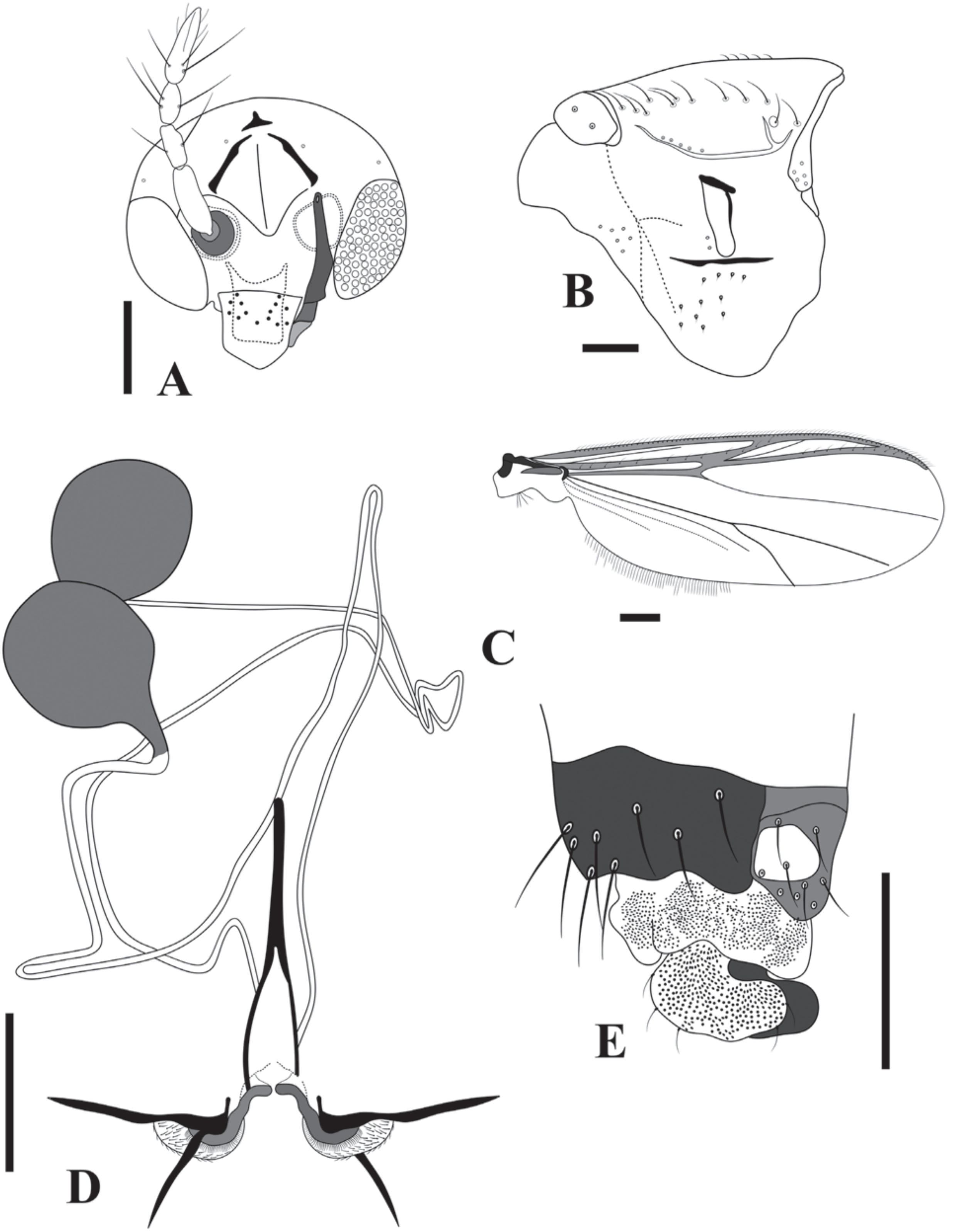


Figure 9. *Limnophyes stagnum* sp. nov., adult female **A** head **B** thorax **C** genitalia ventral **E** genitalia dorsal. Scale bars: 100 μm.

Legs. Fore tibia spur 36–45, 40 μm long, mid tibia spurs 16 and 14 μm long, hind tibia spurs 31 and 24 μm long, hind tibia comb with around 10 spines. Lengths and proportions of legs as in Table 3.

Table 3. Male leg lengths (µm) and proportions of *Limnophyes stagnum* sp. nov.

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR	BV	SV
P_1	469	541	278	163	104	60	69	0.50	3.3	3.6
P_2	496	471	205	116	69	47	63	0.40	4.0	4.7
P_3	447	515	282	150	118	41	68	0.50	3.3	3.4

Hypopygium (Fig. 8E). Anal point extremely short, almost receded, wide, and triangular with apex rounded; anal point 6–15, 10 µm long and 14–34, 24 µm wide. Virga bifid and short, 11–12 µm long. Transverse sternapodeme with well-developed oral projections; sternapodeme 75–79, 77 µm long. Phallapodeme 28–40, 34 µm long. Inferior volsella small triangular lobe covered in numerous simple setae. Gonostylus expanded evenly from base to apex, 67–73, 70 µm long; crista dorsalis very narrow. Gonocoxite 90–116, 103 µm long. HR 1.2–1.7, 1.5, HV 2.5–2.9, 2.7.

Female (*n* = 3). Total length 1.7–1.8 mm. Wing 0.96 mm long, 0.38 mm wide.

Coloration. Same as the male.

Head (Fig. 9A). Antenna with 4 flagellomeres, last flagellomere with 4 sensilla chaetica, Antennal segments 1–4 (in µm): 75–77, 76; 49, 47, 87, AR 0.5. Eyes bare. Temporal setae 2, including 1 inner vertical and 1 frontal. Tentorium 141–145, 143 µm long. Clypeus triangular, 59 µm long and 46 µm wide, bearing 13 setae, setae 37–59, 47 µm long. Palpal segment lengths (in µm): 46, 32, 52, 54, 75.

Thorax (Fig. 9B). Acrostichals 5; dorsocentrals 8–12, 9 in a single row; prealars 5; scutellars 4 in single row; 1 humerals, non-lanceolate; 2 prescutellars non-lanceolate; 7 antepronotals; 2 posterior anepisternals II; 6 epimeron II; 11 preepisternals, 9 clustered horizontally close to epimeron, 4 horizontally arching close to anapleural suture.

Wing (Fig. 9C). Brachiolum with 1 seta. Squama bare. R with 3–8, 5 setae, R_1 with 4–5 setae; R_{4+5} with 9–10 setae; other veins bare. Costa extension 50–74, 62 µm. Microtrichia visible at 10 × magnification.

Legs. Hind and mid femur with keel. Fore tibia spur 22–23 µm long, mid tibia spur 21 µm long, second one broken; hind tibia missing. Lengths and proportions of legs as in Table 4.

Table 4. Female leg lengths (µm) and proportions of *Limnophyes stagnum* sp. nov.

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR	BV	SV
P_1	358	440	224	135	86	51	22	0.50	3.0	3.6
P_2	440	427	190	90	61	39	64	0.40	4.2	4.6
P_3	–	–	–	–	–	–	–	–	–	–

Genitalia (Figs 9D, E). Seminal capsules 62–89, 72 µm long, and 47–90, 71 µm wide, semi-circular; spermathecal very long, with well-developed bulb (Fig. 9D). Notum 76–113, 92 µm long, notum and ramus 143–191, 165 µm long. Gonapophysis VIII divided into ventrolateral and thin dorsomesal lobe (Fig. 9D). Apodeme lobe not distinct. Gonocoxite developed, triangular with around 6–9 setae (Fig. 9E). Tergite IX undivided. Cercus small, pediform, 58–72, 65 µm long, and 42–54, 48 µm wide (Fig. 9E).

Immatures. Unknown.

Etymology. The species is named after the habitat where it is found. The word *stagnum* is Latin, meaning pond or pool.

Distribution. Canada (British Columbia, Ontario); USA (Michigan).

Remarks. This is a very unusual *Limnophyes* species; lack of lanceolate setae on both sexes, lack of humeral setae in males, and single humeral setae in females are distinguishing characteristics. However, the Neotropical species *Limnophyes brachyarthra* (Edwards, 1931) described by Sæther (1990) also lacks lanceolate setae and humerals. The adults of *L. stagnum* sp. nov. can be easily separated from those of *L. brachyarthra* based on the number of antennal flagellomere and AR. Additionally, the chaetotaxy of the thorax varies between the two species, and adult males have gonostylus of different shapes and sizes. According to Sæther (1985) the placement of lanceolate humeral setae in relation to the humeral pit varies among *Limnophyes* species. The lanceolate setae can be in or on the margin of humeral pit, concentrated around or above the pit, or scattered over the humerals. Although the lanceolate setae are missing in *L. stagnum* sp. nov., the humeral seta of the female is located on the pit, similar to that in *L. natalensis*. The shape of the hypopygium of the new species also resembles *Limnophyes natalensis* Kieffer, 1914 as well as *Limnopyes difficilis* Brundin, 1947. The adult male of the new species can be separated from the adult males of *L. natalensis* and *L. difficilis* based on the number of antennal flagellomeres, antennal ratio, lack of lanceolate and humeral setae, number and formation of thoracic setation, and bare squama. The adult female of the new species can be separated from the adult females of *L. natalensis* and *L. difficilis* based on the number of humeral setae, number and formation of thoracic setation, bare squama, and size of the notum.

Rheocricotopus **(*s. s.*)** ***angustus*** **Namayandeh & Hudson sp. nov.**

https://zoobank.org/6D74F69B-4827-43E9-9F1F-122B9D9A8D1F
Figs 10–12

Type material. ***Holotype*** 1 male; CANADA, Newfoundland, Terra Nova National Park; Blue Hill Road, 48.598°N, -53.9702°W; leg. E. Perry; 21.v.2013, dep. CBG. Paratypes 2 females, CANADA, Yukon Territory, Ivvavik National Park, 69.169°N, -140.167°W; leg. N. Perry; 29.vi.2014, dep. CBG. ***Paratype*** 1 larva; USA, Michigan, Detroit, Palmer Park, Pond A; 42.42766°N, 83.11741°W; leg. P.L. Hudson; 30.vi.2022, dep. ARC.

Additional material examined. *Rheocricotopus* (*s. s.*) *effusus* (Walker, 1856), 1 male, associated pupa and larval exuviae; USA, South Dakota, Yankton, Ed's Creek, Gavins Point National Fish Hatchery, leg. P.L. Hudson, det. O.A. Sæther, dep. PLH. *Rheocricotopus* (*s. s.*) *effusus* (Walker, 1856), 1 male, associated pupa and larva exuviae; USA, South Dakota, Yankton, Ed's Creek, Gavins Point National Fish Hatchery, 11.x.1971, leg. P.L. Hudson, dep. PLH. *Rheocricotopus* (*s. s.*) *effusoides* Sæther, 1985, 1 male, associated pupa and larva exuviae; USA, South Dakota, Yankton, Marne Creek, 12.iii.1972, leg. P.L. Hudson, dep. PLH. *Rheocricotopus* (*s. s.*) *unidentatus* Sæther & Schnell, 1988, 1 larva. GERMANY,

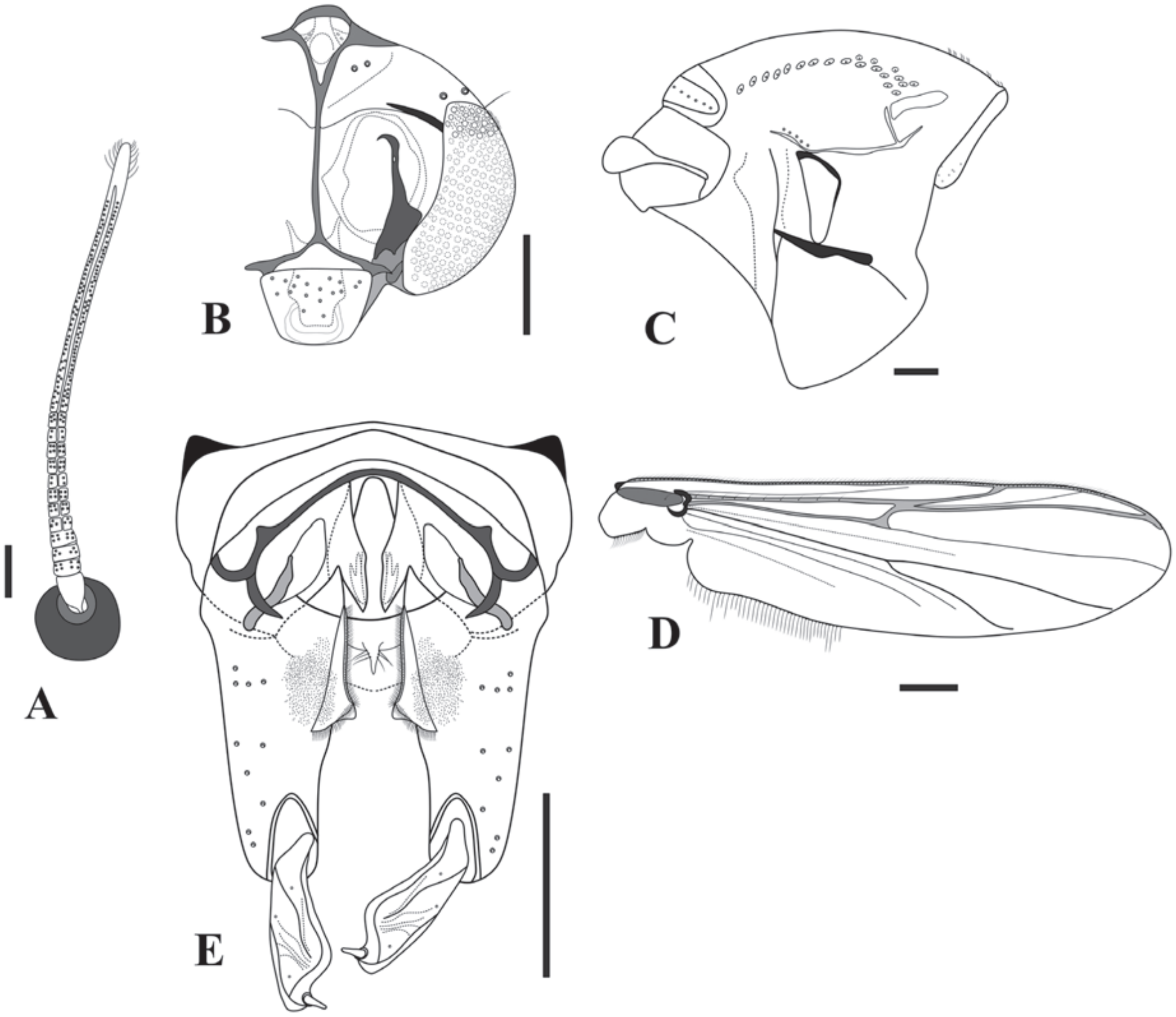


Figure 10. *Rheocricotopus* (*s. s.*) *angustus* sp. nov., adult male **A** antenna **B** head **C** thorax **D** wing **E** hypopygium. Scale bars: 100 µm.

Federal State Hessen, Freiensteinau, Nature Park Vogelsberg, (north-east f. Frankfurt), forest spring, 02.iv.2017, leg. T. Bendt, dep. TB. *Rheocricotopus* (*s. s.*) *pauciseta* Sæther, 1969, holotype, 1 male, associated pupa and larval exuviae; CANADA, British Columbia, Marion Lake, University of British Columbia Forestry Farm, Haney, small mountain stream, 15.vii.1967, leg., A. L. Hamilton and O. A. Sæther, dep. CNC, No. 9990.

Diagnostic characters. *R. angustus* sp. nov. can be separated from other *Rheocricotopus* by the combination of the following characteristics: Adults with elongate ellipsoid humeral pits, without smaller basal pit, narrowing at the base for the male. Adult male with AR 1.4, anal point very short with 6 lateral setae, superior volsella with caudomedian projection strongly bent, thick, short and triangular. Adult female with AR 0.29, costa extension 115–119 µm long, notum 207–228 µm long. Fourth instar larva with AR 2.2, SI bifid with equal branches, SII long and thin, 37 µm long, mentum's cardinal beard with 27 setae, seta submenti very long.

Description. Male (*n* = 1). Total length 3.3 mm. Wing 1.8 mm long and 0.55 mm wide.

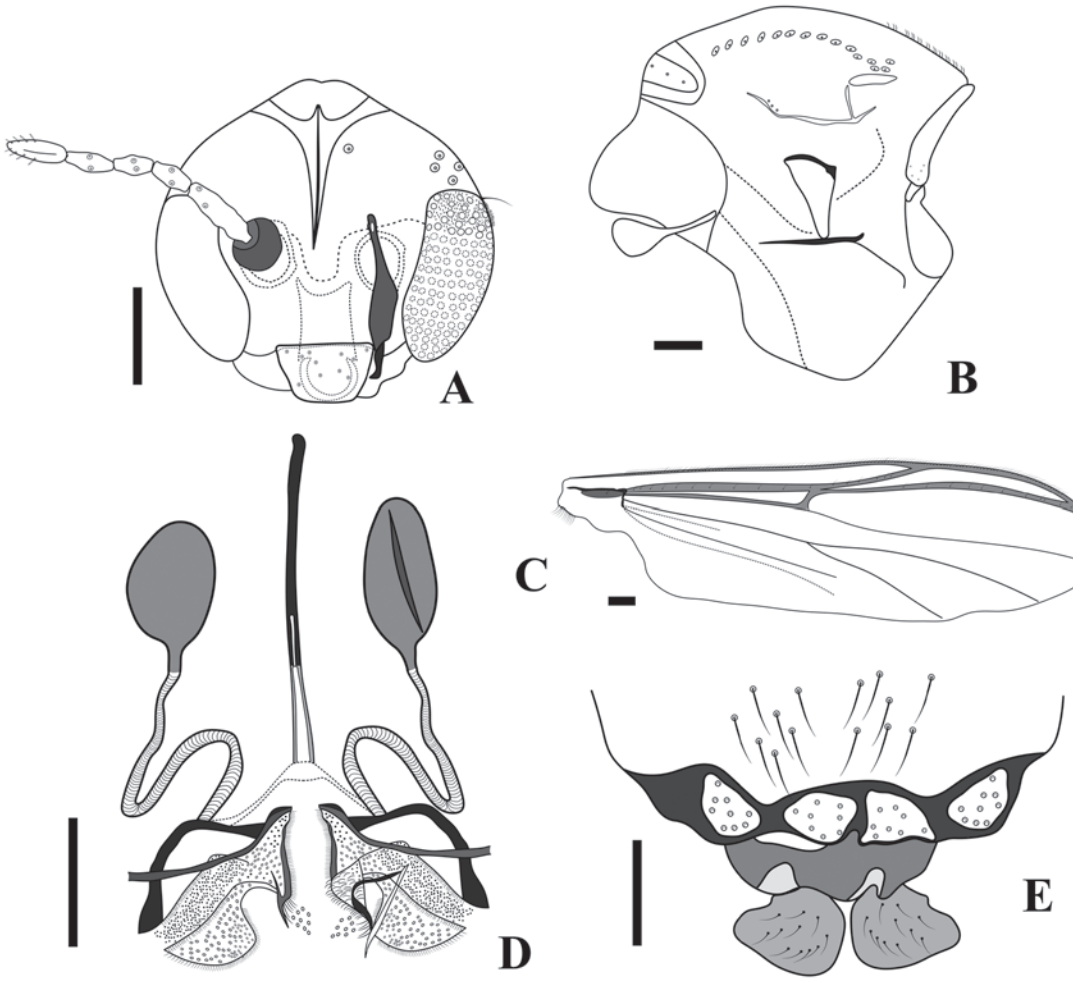


Figure 11. *Rheocricotopus* (*s. s.*) *angustus* sp. nov., adult female **A** head **B** thorax **C** wing **D** genitalia ventral **E** genitalia dorsal. Scale bars: 100 μm.

Coloration. Head, thorax, halters, legs, tergites, sternites, and hypopygium blackish brown. Wings pale brown.

Head (Fig. 10A, B). Antenna with 13 flagellomeres, last flagellomere with 14 sensilla chaetica, groove starts at 4th flagellomere (Fig. 10A), AR 1.4 (*n* = 1). Eyes hairy, without dorsomedial extension. Temporal setae 5, including 2 frontals, 2 postoculars and 1 outer vertical. Tentorium 178 μm long (Fig. 10B). Clypeus rectangular, 89 μm long and 136 μm wide, bearing 18 setae, setae 56–65, 60 μm long. Palpal segment lengths (in μm): 97, 69, 122, 135, 190. Third palpomere with single thin sensilla clavata.

Thorax (Fig. 10C). Acrostichals 12, start close to antepronotum; dorsocentrals 19–20; prealars 5; scutellars 12 in single row; antepronotals 7. Humeral pit elongate ellipsoid narrowing at the base, about half the size of antepronotum, and no smaller basal pit.

Wing (Fig. 10D). Brachiolum with 1 seta. Squama with 13 setae. R with 10 setae; all other veins bare. Costa extension is 44 μm long. Anal lobe developed.

Legs. Fore tibia spur and tarsal segments missing, mid tibia spurs 26 and 22 μm long, hind tibia spurs 55 and 17 μm long, hind tibia comb with 13 spines. Lengths and proportions of legs as in Table 5.

Table 5. Male leg lengths (µm) and proportions of *Rheocricotopus* (*s. s.*) *angustus* sp. nov.

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR	BV	SV
P_1	824	857	–	–	–	–	–	–	–	–
P_2	767	782	375	219	144	95	104	0.50	3.4	4.1
P_3	739	912	516	291	229	121	116	0.60	2.9	3.2

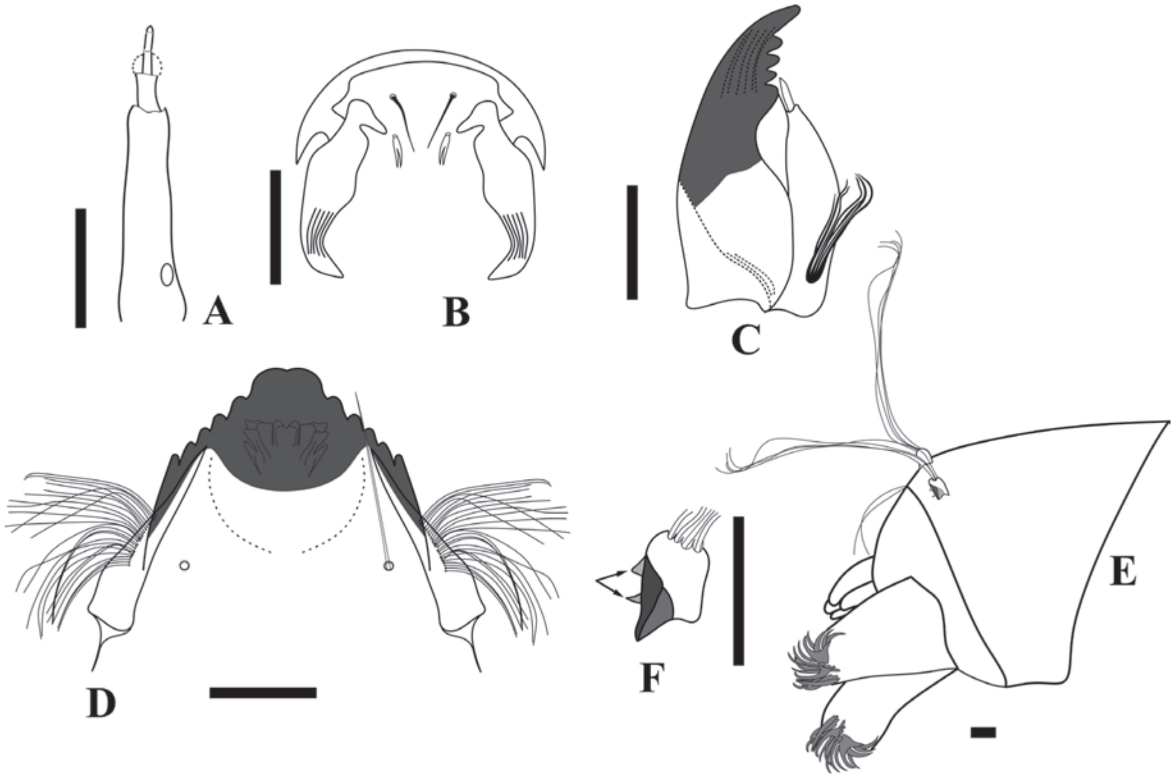


Figure 12. *Rheocricotopus* (*s. s.*) *angustus* sp. nov., fourth instar larva **A** antenna **B** labrum and premandible **C** mandible **D** mentum **E** posterior portion of the larva **F** procercus, arrows indicate the tubercles. Scale bars: 50 µm.

Hypopygium (Fig. 10E). Laterosternite IX 62 µm long, with 12 setae. Anal point very short, 19 µm long and 14 µm wide at the base, triangular with apex pointed and with 6 lateral setae. Transverse sternapodeme with well-developed oral projections; sternapodeme 135 µm long. Phallapodeme 48 µm long. Superior volsella with caudomedian projection tick, short and triangular, parallel but not touching in middle, strongly bent, 35 µm long. Inferior volsella triangular lobe covered in numerous simple setae, apex slightly bent. Gonocoxite 208 µm long. Gonostylus 98 µm long; crista dorsalis very large covering more than half of gonostylus, mega setae 12 µm long. HR 2.1, HV 3.4.

Female (*n* = 2). Total length 1.8–2.5, 2.2 mm. Wing 1.5–1.9, 1.7 mm long and 0.56–0.61, 0.58 mm wide.

***Coloration*.** Same as the male.

Head (Fig. 11A). Antenna with 5 flagellomeres, last flagellomere with 6 sensilla chaetica, Antennal segments 1–5 (in µm): 71–101, 86; 42–55, 48; 39–48, 44; 62; 78; AR 0.29. Eyes hairy, reniform. Temporal setae 5 including 1 frontal, 2 outer verticals, and 2 postoculars. Tentorium 144–174, 159 µm long. Clypeus rectangular, 65–82, 74 µm long and 96–110, 104 µm wide, bearing 12 setae,

setae 53–63, 59 µm long. Palpal segment lengths (in µm): 27–31, 29; 31–34, 32; 57–71, 64; 61; 72–90, 81.

Thorax (Fig. 11B). Acrostichals 21; dorsocentrals 12–18, 15, in a single row; prealars 3; scutellars 6 in single row; antepronotals 5. The humeral pit is similar to that of the male but not narrow at the base.

Wing (Fig. 11C). Brachiolum with 1 seta. Squama with 10 setae. R with 10 setae; R_1 with 5–8, 7 setae; R_{4+5} 9–14, 12 setae; other veins without setae. Costa extension 115–119, 117 µm.

***Legs*.** Fore tibia spur missing, mid tibia spurs 17 and 21 µm long, hind tibia spurs 17 and 36 µm long; hind tibia comb with around 13 spines. The lengths and proportions of the legs are shown in Table 6.

Table 6. Female leg lengths (µm) and proportions of *Rheocricotopus* (*s. s.*) *angustus* sp. nov.

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR	BV	SV
P_1	491	513	–	–	–	–	–	–	–	–
P_2	576	522	213	130	98	59	75	0.41	3.6	5.2
P_3	610	666	–	–	–	–	–	–	–	–

Genitalia (Fig. 11D, E). Seminal capsules ovoid, 82–119, 102 µm long, and 56–80, 66 µm wide; spermathecal ducts without loop, with well-developed bulb. Notum 207–228, 218 µm long, notum and ramus 256–285, 270 µm long. Gonapophysis VIII divided into large ventrolateral covering smaller dorsomesal lobe. Apodeme lobe distinct. Gonocoxite developed, with around 8 setae (Fig. 11E). Tergite IX divided in two pale ovoid sections each bearing around 8–9 setae. Cercus large, base semi-circular, apex pediform, 66–89, 78 µm long, and 71–96, 83 µm wide.

Immatures. The pupa is unknown. The larva is associated by molecular DNA-barcoding.

4th instar larva (*n* = 1). Total length 7.1 mm. Head 354 µm long and 381 µm wide.

***Coloration of the mounted specimen*.** Head capsule yellowish brown with occipital region darker than rest of the head capsule, body greyish brown.

Head (Fig. 12A–D). Antenna 5 segmented; segments length in µm: 86, 14, 10, 7, 7; AR 2.2; basal antennal segment 20 µm wide, distance from the ring organ to base of basal segment 8 µm. Lauterborn organ robust covering the 3rd segment, blade damaged. Labral SI bifid with equal branch, SII–SIII simple, SII long and thin (Fig. 12B). Premandible simple, 78 µm long (Fig. 12B). Mandible much paler in basal half, apical tooth shorter than combined width of three inner teeth; seta subdentalis reaches the base of first inner tooth; setae interna with several long branches (Fig. 12C), mandible 137 µm long. Mentum dark, with large median tooth and 5 pairs of lateral teeth, median tooth slightly notched (possibly worn off), median tooth 35 µm wide, 3.6 × the 1st lateral teeth; seta submenti very long, upright reaching the base of median tooth, base aligned with the 4th inner teeth (Fig. 12D); mentum 92 µm long and 134 µm wide; ventromental plate large, extended beyond the mentum, 116 µm long, and 29 µm wide, cardinal beard with 27 lateral setae. Postmentum 242 µm long.

Abdomen (Fig. 12E, F). Posterior parapods 301 µm long and 208 µm long, bearing around 15 simple claws. Procercus 34 µm long and 18 µm wide, bearing two small basal spurs and 4 apical setae (Fig. 12F), apical setae 447 µm long, supraanal setae 49 µm long. 4 anal tubules present, 78–92 µm long.

Etymology. The new species is named after the city of Detroit. The name of the city comes from the French word *détroit* meaning strait or river, which translates to *angustus* in Latin.

Distribution. Canada (Manitoba, New Brunswick, Newfoundland, Nunavut, Ontario, Yukon Territory); USA (Michigan).

Remarks. Based on the shape of superior volsella, *R. angustus* sp. nov. belongs to the *effusus* group. A detailed examination and comparison of the species in this group is provided by Namayandeh and Beresford (2018). Here, we mentioned that the elongate ellipsoidal shape of the humeral pit of *R. angustus* sp. nov. adults are quite distinguishable from other known species in this group, except *Rheocricotopus* (*s. s.*) *unidentatus* Sæther & Schnell, 1988. However, in *R. angustus* sp. nov., no additional smaller basal pit is present. Another distinguishing characteristic of *R. angustus* sp. nov. male is the very short anal point of the male with few lateral setae. The female of *R. angustus* sp. nov. can be separated from the known females of this group by a lower antennal ratio and longer notum and costa extension.

The key to adult males of the *effusus* group we provided in this study is based on a previous key by Namayandeh and Beresford (2018), which was based on a key by Sæther (1985). The provided key can only partially separate the species in this group. *Rheocricotopus* (*s. s.*) *effusoides* Sæther, 1985 and *Rheocricotopus* (*s. s.*) *effusus* (Walker, 1856) can be separated based on the size and ratio in all life stages (Sæther 1985). *R. unidentatus* is quite distinguishable from other species based on the larval mentum characteristic.

The larva of *R. angustus* sp. nov. can be separated from other known larvae in this group by a higher antennal ratio, a bifid SI with equal branches, and SII 37 µm long. Except for *R. unidentatus*, which has a distinguishing single median mental tooth, there are overlapping characteristics of larvae in this group, which makes their separation difficult. These include but are not limited to the

Table 7. Comparison of some relevant larval characteristics of *Rheocricotopus effusus* group. A_1 = Antennal segment 1, HL = Head length, L = Length, No. = Number, TL = Total length, W = Width; for other abbreviations, see Sæther (1980). All measurements are in µm unless otherwise indicated.

	***R. angustus* sp. nov.**	***R. effusus***	***R. effusoides***	***R. pauciseta***	***R. unidentatus***
TL (mm)	7.1	4–5.2	5.2	–	4.0–7.2
HL	354	430	424–514	400	450–600
AR	2.2	1.5–1.8	1.8–2.1	1.55	1.5–2.0
A_1 L	86	45–64	72–85	62–64	69–87
Basal A_1 W	20	–	19–21	13–18	15–24
Distance from base to RO	8	5	12–15	6–10	8–15
SI	Bifid, even branches	Bifid, uneven branches	Bifid, uneven branches	Bifid*	Bifid, uneven branches
SII L	37	14–22	53	40	19–22
Mentum median tooth	Bifid	Bifid	Bifid	Bifid	Single
No. of cardinal beard setae	27	25–31	32–33	20	28–40
Postmentum L	242	218–226	233–259	234	223–249
Procercus L	34	26–28	41–45	40	30–38
Procercus spurs	Present	Present	–	Present	Present
No. procercus apical setae	4	4–5	–	5	5–6
Apical setae L	447	160	549–567	354	450–563

* The labral SI of the examined larvae appears bifid. However, the length of the branches is hard to detect due to the condition of the mount.

length of the head, postmentum, and basal antennal segment, and number cardinal beard setae (Table 7). However, *R. effusus* and *Rheocricotopus pauciseta* Sæther, 1969 are in the lower range of the basal antennal length in comparison to other known larvae of this group. *R. unidentatus* and *R. effusoides* are in the higher range of cardinal beard setae than other species in this group, and *R. angustus* sp. nov. and *R. pauciseta* are in the lower range. We found that the length and shape of labral SII could also distinguish the larvae in this group (see Table 7). We examined the larval procercus of all species in this group, except for the voucher specimen of *R. effusoides*, in which the abdomen was missing, and consulted Mr. Thomas Bendt on the larva of *R. unidentatus* from Germany, which confirms that all larvae possess a pair of small procercal spurs. However, the shape and size of these spurs are very similar (Table 7).

Key to the adult male of *Rheocricotopus effusus* group

1 Superior volsella triangular without distinct caudomedian projection. Inferior volsella distally divided into 2 lobes (Sæther 1969: fig. 47)................... ....**R. (R.) *pauciseta* Sæther**

– Superior volsella with distinct caudomedian projection. Inferior volsella simple..**2**

2 Humeral pit small (Namayandeh and Beresford 2018: fig. 2c). Superior volsella with long finger-like caudomedian projection that meet medially (Namayandeh and Beresford 2018: fig. 3b, c)...**3**

– Humeral pit large. Superior volsella conical with short tapered caudomedian projection...**4**

3 Antennal ratio 0.72–0.79. Anal Point 67 μm long with 12–19 lateral setae (Namayandeh and Beresford 2018: fig. 3b). Caudomedian projection evenly curved (Namayandeh and Beresford 2018: fig. 3c).......................... .... **R. (R.) *reduncusoides* Namayandeh & Beresford**

– Antennal ratio 0.83–1.17. Anal Point 38 μm long with 6–11 lateral setae (Sæther and Schnell: fig. 3b). Caudomedian projection bent (Namayandeh and Beresford 2018: fig. 4a–c; Sæther and Schnell 1988: fig. 1D) ....**R. (R.) *reduncus* Sæther & Schnell**

4 Anal point very short, 19 μm long, with 6 lateral setae (Fig. 10E, F) ....**R. (R.) *angustus* sp. nov.**

– Anal point long, ≥ 40 μm long, usually with > 6 lateral setae......................**5**

5 Anal point 75–98 μm long, with 15–19 lateral setae (Sæther 1986: fig. 18D). Antennal ratio AR 1.4–1.7......................... **R. (R.) *effusoides* Sæther***

– Not with the above combination of characters...**6**

6 Dorsocentrals 18–22. Acrostichals 30–36, reaching 26–38 μm in length. Humeral pit elongated ellipsoid, along the axis of antepronotum (Sæther and Schnell 1988: fig. 3B)................ **R. (R.) *unidentatus* Sæther & Schnell***

– Dorsocentrals 9–16. Acrostichals 18–26, reaching 15–26 μm in length. Humeral pit large, rounded ellipsoid, perpendicular to antepronotum (Lehman 1969: abb. 13A)... **R. (R.) *effusus* (Walker)***

---

* See comments in the remarks section.

Subfamily Chironominae

***Chironomus* nr. sp. *parariparius* of Martin (2023)**

Figs 13A–E

Material examined. 1 male; USA, Michigan, Detroit, Palmer Park, Pond A; 42.42766°N, 83.11741°W; leg. P.L. Hudson; 30.vi.2022, dep. ARC.

Diagnostic characters. The adult male of *C.* nr. sp. *parariparius* can be separated from other *Chironomus* species by the combination of the following characteristics: AR 3.1; frontal tubercle present, 12 μm long; wing without any pattern; fore tibia scale 60 μm long; tergite IX with 9 median setae on two adjacent pale patches; superior volsella S-type, with robust apex and base with 5 long setae.

Description. Male (*n* = 1). Total length 7.0 mm. Wing 3.6 mm long and 0.90 mm wide.

Coloration of the mounted specimen. Head brown. Thorax brown, with scutellum and humeral region pale yellowish. Abdominal tergites with posterior 2/3rd brown and the anterior 1/3rd pale yellowish (Fig. 13A). Halter and wing pale brown.

Head (Fig. 13B, C). Antenna with 11 flagellomeres, the last flagellomere with 4 sensilla chaetica (Fig. 13B), each of 2nd–4th antennal flagellomere with a pair of long sensilla chaetica; groove starts at 4th flagellomere, AR 3.1. Eyes bare, with well-extended dorsomedial extension. Frontal tubercle present, 12 μm long. Temporal setae 25, uniserial. Tentorium 201 μm long. Clypeus nearly squared, 130 μm long and 146 μm wide, bearing 36 setae, setae 108 μm long. Palpal segment lengths (in μm): 216, 116, 272, 234, 337. Third palpomere with 7 sensilla clavata.

Thorax. Acrostichals 2, close to antepronotum; dorsocentrals 14 in single row; prealars 5; scutellars 14 in double rows; antepronotals 1. Mid-scutum hump is present.

Wing (Fig. 13D). Wing without any pattern. Brachiolum with 1 seta, squama with 17 setae, R with 40 setae, R_1 with 47 setae, R_{4+5} with 65 setae. Anal lobe developed.

Legs. Mid and hind legs missing. Fore tibia scale 60 μm long. The lengths and proportions of the legs as in Table 8.

Table 8. Male leg lengths (μm) and proportions of *Chironomus* nr. sp. *parariparius* by Martin, 2023.

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR	BV	SV
P_1	1552	1328	2144	1216	903	722	338	1.6	1.6	1.3
P_2	–	–	–	–	–	–	–	–	–	–
P_3	–	–	–	–	–	–	–	–	–	–

Hypopygium (Fig. 13E). Tergite IX with 12 median setae, seven on adjacent small pale patches and 5 more posteriorly without pale patches, all pointing toward anal point. Anal point broad, parallel-sided with a round apex, 119 μm long. Sternapodeme squared, 129 μm long. Phallapodeme 202 μm long. Superior volsella S-type with robust apex, and base with 5 long setae, 83 μm long. Inferior volsella 178 μm long, base slightly bent, apex reaches the mid-section of the anal point. Gonocoxite 111 μm long. Gonostylus 204 μm long, with 5 long setae at apex; HR 0.5, HV 2.6.

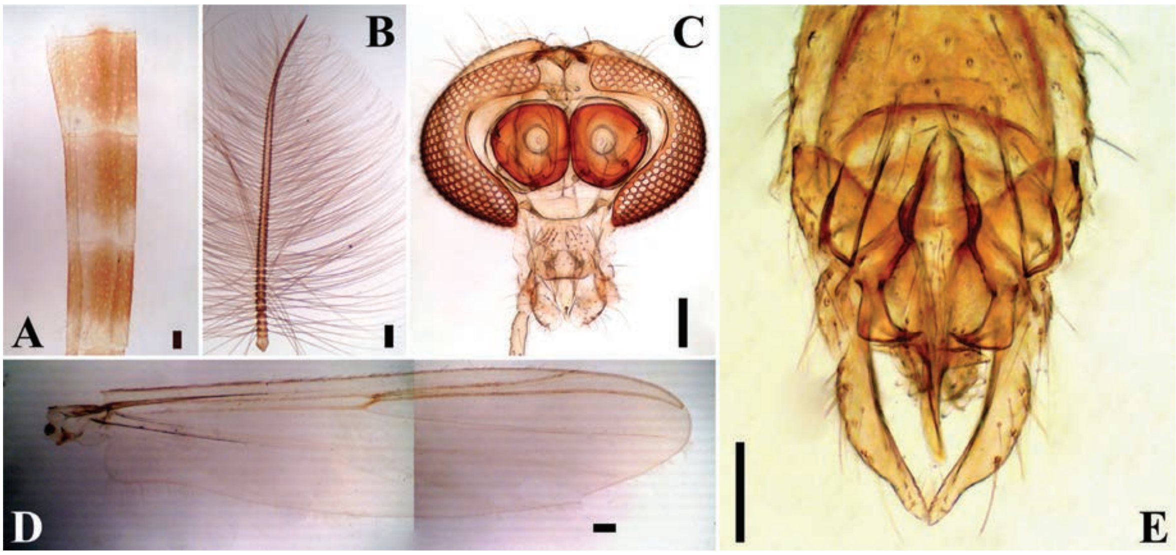


Figure 13. *Chironomus* nr. sp. *parariparius* of Martin (2023), adult male **A** abdominal tergites III–V **B** antenna **C** head **D** wing **E** hypopygium. Scale bars: 100 µm.

Remarks. The single adult male of the *Chironomus* species we collected from Pond A closely resembles the *Chironomus* species Martin (2023) described as Species 2c. or *Chironomus* species *parariparius*. According to Martin (2023), only the images of the adult male are available based on the reared collection of specimens by J.E. Sublette, now kept in the Zoological Museum of the University of Minnesota, St. Paul. Pupa is only described by the caudolateral spur of segment VIII; however, larva morphology and cytology are described by Martin (2023) in detail. Martin (2023) describes the species' habitat as snow pools, similar to Pond A. The adult male from pond A is quite distinguishable from other species in the *C. riparius* group based on the characteristics of the hypopygium (Jon Martin, pers. comm. 18 March 2024).

Polypedilum (*s. s.*) sp.

Remarks. The adult males of the *Polypedilum* (*s. s.*) specimens that we collected from Pond A resemble *Polypedilum* (*s. s.*) *trigonus*, Townes, 1945. However, these adults did not key out to any known Nearctic adult male in the subgenus *Polypedilum* based on Maschwitz and Cook (2000). The adult male of this species is distinguished by the following characteristics: head, thorax, and abdomen uniformly dark brown, legs stramineous; AR 1.8; wing unmarked; anal point extending to or slightly higher than inferior volsella; superior volsella without tubercle, sickle-shaped, robust at the base narrowing and bent at apex; inferior volsella tubular and narrow. Based on the molecular data obtained, the species does not match any known *Polypedilum* species in GenBank or BOLD, only to sequences identified only as *Polypedilum* sp., accession numbers HQ982463 and HQ981830. The adult males obtained in this study possibly represent a new species. However, we need to examine more materials, including those of the related species, before we can make the decision on the status of this species. The hypopygium of the adult male is shown in Fig. 6P.

Discussion

Vernal pools and, in fact, many isolated or temporary habitats can be easily ignored as insignificant marginal environments. Although ephemeral in their hydrological nature, they are permanent landscape features like other lotic and lentic habitats (Zedler 2003). In an urban environment, these permanent landscape features are likely remnants of a greater ecosystem and, as such, can provide refugia or connecting corridors for a naturally occurring population of species (Dearborn and Kark 2010). Natural areas in city parks surrounded by built-up urban areas can also act as island-like environments in which rapid evolution can occur (Jackson et al. 2022). What we demonstrated in this study is that often overlooked urban natural habitats, such as Palmer Park in a large Detroit metropolitan area, can produce fascinating biological discoveries. These discoveries include new species and faunistic records that would have otherwise been ignored due to a lack of interest in the biodiversity value of urban natural habitats. Further, the discovery of new species and new faunistic records demonstrate the importance of conserving temporary aquatic habitats such as the vernal pools. The public, and in our case, students, are often fascinated with the presence of new species and record discoveries (see DeGasparro et al. 2020). This fascination not only has an educational value for them but also motivates them to engage in the study and conservation of their local natural habitats.

Acknowledgments

We gratefully acknowledge the help and cooperation we received from many dedicated researchers and express our sincere thanks to all of these, without whom this work would not have been possible: Dr. Jon Martin of the University of Melbourne for help on the taxonomy of *Chironomus* species; Mr. Thomas Bendt, Heyerhütte, Germany for help on larval taxonomy; Dr. Scott Brooks, and Diptera researchers and staff at the Canadian National Collection of Insects, Arachnids, and Nematodes; Niloufar Arfaeimoghaddam, Allison Brown, Rebekah Hest, Valerie Levesque-Beaudin, Claudia Steinke, and staff and researchers at Centre for Biodiversity Genomics, University of Guelph; Dr. Elisabeth Stur of the Department of Natural History, NTNU University Museum, Norway; Dr. Anthony Cognato and Dr. Sarah Smith of the A.J. Cook Arthropod Research Collection, Michigan State University, for housing the type and voucher specimens; Mr. James Hartrick, and staff and technicians at LimnoTech for the environmental data; Staff and Personnel of Palmer Park and Detroit Exploration & Nature Center for their logistic support; Wayne State University UROP (Undergraduate Research Opportunity); Dr. Jeff Pu, Water Innovation, Cleveland Water Alliance for installing the sensors and the water chemistry; our reviewers who helped improving this article.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

Funding for this study was provided by the Sharon L. Ram Aquatic Sciences Fund of the Community Foundation of Southeast Michigan, the City of Detroit Parks and Recreation Department, and Healthy Urban Waters for the purchase of the equipment used in the Palmer Park Field Laboratory at the DEN.

Author contributions

All authors have contributed equally.

Author ORCIDs

Armin Namayandeh https://orcid.org/0000-0003-2136-0497
Sergio Guerra https://orcid.org/0009-0009-7614-5314
Natasha Islam https://orcid.org/0009-0009-8270-4004
Patrick L. Hudson https://orcid.org/0000-0002-7646-443X
Edris Ghaderi https://orcid.org/0000-0002-9875-7735
Thameena Yusuf https://orcid.org/0009-0000-6296-6693
Adrian A. Vasquez https://orcid.org/0000-0002-2434-3388
Jeffrey L. Ram https://orcid.org/0000-0002-1063-546X

Data availability

The data associated with the new sequences are available in BOLD database (http://dx.doi.org/10.5883/DS-DTPPA). All other data that support the findings of this study are available in the main text or Supplementary Information.

References

Ashe P, O'Connor JP (2012) A World Catalogue of Chironomidae (Diptera). Part 2. A & B Orthocladiinae. Irish Biogeographical Society and National Museum of Ireland. Dublin, 968 pp.

Bright E (2024) Aquatic Insects of Michigan. Chironomidae Newman, 1834: 379-Non-biting midges. http://www.aquaticinsects.org/sp/Diptera/sp_dom_chir.html [Accessed 20 04 2024]

Cadmus P, Pomeranz JPF, Kraus JM (2016) Low-cost floating emergence net and bottle trap: Comparison of two designs. Journal of Freshwater Ecology 31(4): 653–658. https://doi.org/10.1080/02705060.2016.1217944

Caldwell BA, Hudson PL, Lenat DR, Smith DR (1997) A Revised Annotated Checklist of the Chironomidae (Insecta: Diptera) of the Southeastern United States. Transactions of the American Entomological Society 123: 1–53.

Cartwright J, Morelli TL, Grant EHC (2022) Identifying climate-resistant vernal pools: Hydrologic refugia for amphibian reproduction under droughts and climate change. Ecohydrology 15(5): e2354. https://doi.org/10.1002/eco.2354

Chimeno C, Rulik B, Manfrin A, Kalinkat G, Hölker F, Baranov V (2023) Facing the infinity: Tackling large samples of challenging Chironomidae (Diptera) with an integrative approach. PeerJ 11: e15336. https://doi.org/10.7717/peerj.15336

Chromas (2024) Free trace viewer software for simple DNA sequencing projects. http://www.technelysium.com.au/chromas.html [accessed 20 04 2024]

Colburn EA (2004) Vernal pools: natural history and conservation. The McDonald and Woodward Publishing Company, Granville, OH, USA, 426 pp.

Cornette R, Motitsoe SN, Mlambo MC (2022) A new desiccation-resistant midge from ephemeral rock pools in South Africa, *Polypedilum* (*Pentapedilum*) *cranstoni* sp. nov.

(Diptera: Chironomidae). Zootaxa 5128(3): 397–410. https://doi.org/10.11646/zootaxa.5128.3.5

Cranston PS, Oliver DR (1988) Additions and corrections to the Nearctic Orthocladiinae (Diptera: Chironomidae). The Canadian Entomologist 120: 425–462. https://doi.org/10.4039/Ent120425-5

Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and high-performance computing. Nature Methods 9: 772. https://doi.org/10.1038/nmeth.2109

Dearborn DC, Kark S (2010) Motivations for conserving urban biodiversity. Conservation Biology 24(2): 432–440. https://doi.org/10.1111/j.1523-1739.2009.01328.x

DeGasparro SL, Namayandeh A, Beresford DV (2020) The Value of Local Farms for Insect Conservation: Local Teaching Opportunities. American Entomologist (Lanham, Md.) 66(3): 20–22. https://doi.org/10.1093/ae/tmaa035

Delettre YR (1986) La colonisation de biotopes multiples: Une alternative à la résistance in situ aux conditions mésologiques défavorables. Cas de *Limnophyes minimus* (Mg.), Diptére Chironomidae à larves édaphiques des landes armoricaines. Revue d'Écologie et de Biologie du Sol 23: 29–38.

de Waard JR, Ratnasingham S, Zakharov EV, Borisenko AV, Steinke D, Telfer AC, Perez KH, Sones JE, Young MR, Levesque-Beaudin V, Sobel CN, Abrahamyan A, Bessonov K, Blagoev G, deWaard SL, Ho C, Ivanova NV, Layton KKS, Lu L, Manjunath R, McKeown JTA, Milton MA, Miskie R, Monkhouse N, Naik S, Nikolova N, Pentinsaari M, Prosser SWJ, Radulovici AE, Steinke C, Warne CP, Hebert PDN (2019) A reference library for Canadian invertebrates with 1.5 million barcodes, voucher specimens, and DNA samples. Scientific Data 6(1): 308. https://doi.org/10.1038/s41597-019-0320-2

Donato M, Mauad M, Siri A (2024) New species of *Bryophaenocladius* Thienemann, 1934 (Diptera: Chironomidae) from Argentina. Zootaxa 5448(2): 283–291. https://doi.org/10.11646/zootaxa.5448.2.8

Epler JH (2012) A brachypterous *Bryophaenocladius* (Diptera: Chironomidae: Orthocladiinae) with hypopygium inversum from Heggie's Rock, Georgia, USA. Zootaxa 3355(1): 51–61. https://doi.org/10.11646/zootaxa.3355.1.3

Failla AJ, Vasquez AA, Hudson P, Fujimoto M, Ram JL (2016) Morphological identification and COI barcodes of adult flies help determine species identities of chironomid larvae (Diptera, Chironomidae). Bulletin of Entomological Research 106(1): 34–46. https://doi.org/10.1017/S0007485315000486

Folmer RHA, Nilges M, Folkers PJM, Konings RNH, Hilbers CW (1994) A model of the complex between single-stranded DNA and the single-stranded DNA binding protein encoded by gene V of filamentous bacteriophage M13. Journal of Molecular Biology 240(4): 341–357. https://doi.org/10.1006/jmbi.1994.1449

Frouz J, Matena J, Ali A (2003) Survival strategies of chironomids (Diptera: Chironomidae) living in temporary habitats: a review. European Journal of Entomology 100(4): 459–466. https://doi.org/10.14411/eje.2003.069

Griffiths-Lee J, Nicholls E, Goulson D (2022) Sown mini-meadows increase pollinator diversity in gardens. Journal of Insect Conservation 26(2): 299–314. https://doi.org/10.1007/s10841-022-00387-2

Grodhaus G (1976) Two species of *Phaenopsectra* with drought-resistant larvae (Diptera: Chironomidae). Journal of the Kansas Entomological Society 49(3): 405–418.

Hebert PDN, Ratnasingham S, Zakharov EV, Telfer AC, Levesque-Beaudin V, Milton MA, Pedersen S, Jannetta P, deWaard JR (2016) Counting animal species with DNA barcodes: Canadian insects. Philosophical Transactions of the Royal Society B, Biological Sciences 371(1702): 20150333. https://doi.org/10.1098/rstb.2015.0333

Hinton HE (1960) Cryptobiosis in the larva of *Polypedilum vanderplanki* Hint. (Chironomidae). Journal of Insect Physiology 5(3–4): 286–300. https://doi.org/10.1016/0022-1910(60)90011-1

Jackson N, Littleford-Colquhoun BL, Strickland K, Class B, Frere CH (2022) Selection in the city: Rapid and fine-scale evolution of urban eastern water dragons. Evolution; International Journal of Organic Evolution 76(10): 2302–2314. https://doi.org/10.1111/evo.14596

Jones RE (1975) Dehydration in an Australian rockpool chironomid larva, (*Paraborniella tonnoiri*). Journal of Entomology Series A, General Entomology 49(2): 111–119. https://doi.org/10.1111/j.1365-3032.1975.tb00074.x

Kimura M (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. Journal of Molecular Evolution 16(2): 111–120. https://doi.org/10.1007/BF01731581

Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: Molecular evolutionary genetics analysis across computing platforms. Molecular Biology and Evolution 35(6): 1547–1549. https://doi.org/10.1093/molbev/msy096

Larkin MA, Blackshields G, Brown NP, Chenna R, McGettigan PA, McWilliam H, Valentin F, Wallace IM, Wilm A, Lopez R, Thompson JD, Gibson TJ, Higgins DG (2007) Clustal W and Clustal X version 2.0. Bioinformatics 23(21): 2947–2948. https://doi.org/10.1093/bioinformatics/btm404

Larned ST, Datry T, Arscott DB, Tockner K (2010) Emerging concepts in temporary-river ecology. Freshwater Biology 55(4): 717–738. https://doi.org/10.1111/j.1365-2427.2009.02322.x

Lehmann J (1969) Europaischen Arten der Gattung *Rheocricotopus* Thien und Harn. und drei neue Artvertreter dieser Gattung aus der Orientalis (Diptera, Chironomidae). Archiv für Hydrobiologie 66: 348–381.

Makarchenko EA, Makarchenko MA (2009) New records of chironomids (Diptera, Chironomidae, Orthocladiinae) in Far East and bordering territories. VII. *Bryophaenocladius* Thienemann. Eurasian Entomological Journal 8: 51–63.

Martin J (2023) North American Species of the Genus *Chironomus* as recognized by morphology and larval cytology (includes *Chaetolabis*, *Lobochironomus* and *Einfeldia* (sens. lat.) and species included in *Tendipes* by Townes (1945) but now placed in other genera). https://www.chironomidae.net/Martin/NACytfiles/NAChiron.html [Accessed 20 04 2024]

Maschwitz DE, Cook EF (2000) Revision of the Nearctic species of the genus *Polypedilum* Kieffer (Diptera: Chironomidae) in the subgenera *P.* (*Polypedilum*) Kieffer and *P.* (*Uresipedilum*) Oyewo and Sæther. Ohio Biological Survey Bulletin New Series Vol. 12. Ohio, Hilliard, 135 pp.

McLachlan AJ (1988) Refugia and habitat partitioning among midges (Diptera: Chironomidae) in rain-pools. Ecological Entomology 13(2): 185–193. https://doi.org/10.1111/j.1365-2311.1988.tb00346.x

Miller MA, Pfeiffer W, Schwartz T (2012) The CIPRES science gateway: enabling high-impact science for phylogenetics researchers with limited resources. In: Proceedings of the 1st Conference of the Extreme Science and Engineering Discovery Environment: Bridging from the eXtreme to the campus and beyond. ACM, Chicago Illinois USA, 1–8. https://doi.org/10.1145/2335755.2335836

Namayandeh A, Beresford DV (2017) New range extensions for the Canadian Chironomidae fauna from two urban streams. Chironomus 30(30): 76–80. https://doi.org/10.5324/cjcr.v0i30.2415

Namayandeh A, Beresford DV (2018) A new species in the *Rheocricotopus* (*R.*) *effusus* group from Canada with a review of the Nearctic species of *Rheocricotopus* and *Parametriocnemus* (Chironomidae: Orthocladiinae). Chironomus 31(31): 16–29. https://doi.org/10.5324/cjcr.v0i31.2531

Namayandeh A, Hudson PL (2022) Two new Orthocladiinae (Diptera: Chironomidae) collected in overlooked places of Midwest USA. Zootaxa 5099(1): 120–128. https://doi.org/10.11646/zootaxa.5099.1.5

Oliver DR, Dillon ME, Cranston PS (1990) A Catalog of Nearctic Chironomidae. Research Branch Agriculture Canada, Ottawa, 89 pp.

Owen J, Owen DF (1975) Suburban gardens: England's most important nature reserve? Environmental Conservation 2(1): 53–59. https://doi.org/10.1017/S0376892900000692

Puillandre N, Lambert A, Brouillet S, Achaz G (2012) ABGD, Automatic Barcode Gap Discovery for primary species delimitation. Molecular Ecology 21(8): 1864–1877. https://doi.org/10.1111/j.1365-294X.2011.05239.x

Quistberg RD, Bichier P, Philpott SM (2016) Landscape and local correlates of bee abundance and species richness in urban gardens. Environmental Entomology 45(3): 592–601. https://doi.org/10.1093/ee/nvw025

Rambaut A (2014) FigTree 1.4. 2 software, Institute of Evolutionary Biology. Univ. Edinburgh.

Sæther OA (1969) Some Nearctic Podonominae, Diamesinae and Orthocladiiane. Bulletin - Fisheries Research Board of Canada 170: 154.

Sæther OA (1977) Female genitalia in Chironomidae and other Nematocera: Morphology, phylogenies, keys. Bulletin - Fisheries Research Board of Canada 197: 1–220.

Sæther OA (1980) Glossary of chironomid morphology terminology (Diptera, Chironomidae). Entomologica Scandinavica (Supplement 14): 1–51.

Sæther OA (1985) A review of the genus *Limnophyes* Eaton from the Holarctic and Afrotropical regions (Diptera: Chironomidae, Orthocladiinae). Entomologica Scandinavica (Supplement 35): 1–139.

Sæther OA (1986) A review of the genus *Rheocricotopus* Thienemann & Harnisch, 1932 (Diptera: Chironomidae), with the description of three new species. Spixiana (Supplement 11): 59–108.

Sæther OA (1990) A revision of the Neotropical types described as *Spaniotoma* (*Limnophyes*) by Edwards 1931, with the description of *Edwardsidia* gen. n. (Diptera: Chironomidae). Insect Systematics & Evolution 21(3): 305–319. https://doi.org/10.1163/187631290X00229

Sæther OA, Schnell ØA (1988) Two new species of the *Rheocricotopus* (*R.*) *effusus* group (Diptera, Chironomidae). Spixiana (Supplement): 65–74.

Stamatakis A (2014) RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30(9): 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Suemoto T, Kawai K, Imabayashi H (2004) A comparison of desiccation tolerance among 12 species of chironomid larvae. Hydrobiologia 515(1–3): 107–114. https://doi.org/10.1023/B:HYDR.0000027322.11005.20

Vasquez AA, Bonnici BL, Yusuf SH, Cruz JI, Hudson PL, Ram JL (2022) Improved chironomid barcode database enhances identification of water mite dietary content. Diversity 14(2): 65. https://doi.org/10.3390/d14020065

Wang XH, Liu Z, Epler JH (2004) New species of *Bryophaenocladius* Thienemann from the Nearctic Region (Diptera: Chironomidae: Orthocladiinae). Zootaxa 581(1): 1–10. https://doi.org/10.11646/zootaxa.581.1.1

Williams DD (2006) The Biology of Temporary Waters. Oxford University Press Inc., New York, USA, 336–336.

Zedler PH (2003) Vernal pools and the concept of “isolated wetlands.”. Wetlands 23(3): 597–607. https://doi.org/10.1672/0277-5212(2003)023[0597:VPATCO]2.0.CO;2

Supplementary material 1

List of taxa, codes, GenBank, or BOLD accessions

Authors: Armin Namayandeh, Sergio Guerra, Natasha Islam, Taylor James, Patrick L. Hudson, Edris Ghaderi, Thameena Yusuf, Adrian A. Vasquez, Jeffrey L. Ram

Data type: pdf

Link: https://doi.org/10.3897/zookeys.1208.24495.suppl1

ZooKeys 1208: 165–172 (2024)
DOI: 10.3897/zookeys.1208.128640

Research Article

Dickyyuella argentinensis a tentative new genus and species of Cardiochilinae (Hymenoptera, Braconidae) from the Neotropical region

Ilgoo Kang[1], Michael J. Sharkey[2]

1 Department of Entomology, Kyungpook National University, Sangju, Gyeongsangbuk-do, Republic of Korea
2 The Hymenoptera Institute, Redlands, CA, USA
Corresponding author: Ilgoo Kang (ikang@knu.ac.kr)

Abstract

Dickyyuella Kang & Sharkey, **gen. nov.** is a novel addition to the microgastroid complex of Braconidae. Taxonomic assignment within this complex posed challenges initially due to the presence of putatively plesiomorphic characters. However, closer examination revealed affiliations with the microgastroid complex, supported by morphological features such as the location of spiracles on the first metasomal tergum and the absence of spiracles on the seventh metasomal tergum. Based on the following two morphological characters, the presence of an inverted Y-shaped groove on the first metasomal tergum and pectinate tarsal claws, *Dickyyuella* Kang & Sharkey, **gen. nov.** is tentatively placed within Cardiochilinae Ashmead, 1900 despite uncertainties surrounding phylogenetic relationships. This article provides the diagnosis of *Dickyyuella* Kang & Sharkey, **gen. nov.**, the description of *Dickyyuella argentinensis* Kang & Sharkey, **sp. nov.**, and a discussion of the taxonomic placement of the new genus within the microgastroid complex.

Key words: Argentina, Ichneumonoidea, morphology, Neotropics, new species, non-cyclostomes, parasitoid, taxonomy, wasp

Academic editor: Filippo Di Giovanni
Received: 30 May 2024
Accepted: 26 June 2024
Published: 29 July 2024

ZooBank: https://zoobank.org/61FBFC75-F50A-46AC-BAA2-55F72847EC9E

Citation: Kang I, Sharkey MJ (2024) *Dickyyuella argentinensis* a tentative new genus and species of Cardiochilinae (Hymenoptera, Braconidae) from the Neotropical region. ZooKeys 1208: 165–172. https://doi.org/10.3897/zookeys.1208.128640

Introduction

Members of Braconidae Latreille, 1829 are traditionally divided into two major groups, cyclostomes and non-cyclostomes, depending on the presence/absence of an opening between the clypeus and mandibles (Sharkey 1993). Non-cyclostome members lack this opening, making the labrum mostly invisible. Among the non-cyclostome subfamilies, there is a recently derived group, the microgastroid complex, which comprises seven subfamilies: Cardiochilinae Ashmead, 1900, Cheloninae Föerster, 1863, Dirrhopinae van Achterberg, 1984, Khiokhoiinae Mason, 1983, Mendesellinae Whitfield & Mason, 1994, Microgastrinae Föerster, 1863 and Miracinae Viereck, 1918. All members of the microgastroid complex are known as endoparasitoids of Lepidoptera (Yu et al. 2016). The phylogenetic relationships among the subfamilies of this complex have garnered significant attention from braconidologists, who have attempted to resolve these relationships using morphological characteristics, molecular data, and polydnaviruses (Quicke and van Achterberg 1990; Whitfield and Mason 1994; Whitfield 1997; Dowton and Austin 1998; Murphy et al. 2008). Recent studies based on ultraconserved elements (UCEs) data have resolved Dirrhopinae as a sister taxon to Cheloninae, thereby confirming its placement in the microgastroid complex (Jasso-Martínez et al. 2023).

While examining specimens in the Entomology Research Museum at the University of California, Riverside (UCRC; Riverside, CA, USA), the second author discovered a highly distinctive braconid specimen from the Neotropical region and shared this discovery with a few other braconid experts. Following examinations by each author, we initially hypothesized that the specimen might represent a new braconid subfamily. However, further analysis led us to describe a tentative new genus of Cardiochilinae, *Dickyyuella* Kang & Sharkey, gen. nov., and a new species *Dickyyuella argentinensis* Kang & Sharkey, sp. nov. based solely on a single specimen. This specimen shares some characteristics with other subfamilies of the microgastroid complex and is distinct from the other genera within Cardiochilinae.

Material and methods

The singleton specimen was borrowed from UCRC and examined by both authors. Leica MZ 16 and MZ75 stereomicroscopes were used to the examine specimen. Images of the specimen were taken using a JVC digital camera mounted on the Leica MZ 16 microscope and were stacked using Automontage software (Syncroscopy). The stacked images were then edited using Adobe Photoshop® CS 6 and Photoshop® CC 2024 v. 25.7.0 (Adobe Systems, Inc.). Terms for external morphology and wing venation are based on Sharkey and Wharton (1997). Terms for external sculptures follow Harris (1979). The following are acronyms used in this article except abstract: T1: first metasomal tergum; T2: second metasomal tergum; T7: seventh metasomal tergum. Morphometric characters were measured using Adobe Photoshop® CC 2024 v. 25.7.0. All measurements are provided in millimeters, with numbers in parentheses in the species description representing the actual size of each body part.

Results and discussion

Taxonomy

Dickyyuella Kang & Sharkey, gen. nov.
https://zoobank.org/5FC120A3-326D-423A-8913-3A1C8B673D5B
Fig. 1A–E

Type species. *Dickyyuella argentinensis* Kang & Sharkey, sp. nov.

Diagnosis. Body relatively small compared to members of the other cardiochiline genera, with strong sculpture, especially on mesosoma. Antenna thick (Fig. 1A). Eyes bare (Fig. 1B). Occipital carina well developed dorsally, absent ventrally (Fig. 1E). Most of head with weak microsculpture. Median ocellus surrounded medially and laterally by a smooth, curved ridge. Pronotum bilobed anteriorly with a transverse plate dorsally. Notauli deeply impressed and entirely costate (Fig. 1E). Median lobe of mesoscutum bilobed. Scutellar sulcus deep with a median carina (Fig. 1E). Scutellum smooth and flat. Postscutellar depression absent (Fig. 1E). Epicnemial carina strong and complete (Fig. 1B). Precoxal sulcus well defined with ~5 costulae (Fig. 1B). Propodeum rugose with a large, well-defined median areola. Apical abscissa of RS entirely nebulous and almost straight, very slightly curved posteriorly (Fig. 1C). (RS+M)b about 3 × longer than m-cu vein (Fig. 1C). 1M about 3 × longer than m-cu vein; lacking distinct claval lobe. Veins M+Cu and M about equal in length. Hind basitarsomere swollen (Fig. 1A). Tarsal claws rather large with pectinate base (Fig. 1D). Spiracle of T1 on membranous laterotergite (Fig. 1B). T1 wide with carinate lateral margins; medial area of T1 with an inverse Y-shaped depression (Fig. 1E).

Biology. Unknown.

Distribution. Neotropics.

Etymology. The genus name is a patronym in honor of Dicky Sick Ki Yu, who developed Taxapad and made significant contributions to Braconidae and Ichneumonidae systematics research. Gender is feminine.

Notes. The members of *Dickyyuella* Kang & Sharkey, gen. nov. will run to couplet 1 in the key to the world genera by Dangerfield et al. (1999), but it can be easily distinguished from members of *Heteropteron* and *Neocardiochiles* by the size, well-developed occipital carina, deep and broad notauli, large median areola on propodeum, and rugose propodeum.

Species description

***Dickyyuella argentinensis* Kang & Sharkey, sp. nov.**
https://zoobank.org/C178D89C-B759-4E20-BD20-65946C833E4E

Material examined. ***Holotype*****.** **ARGENTINA** • ♀, Tucumán Pr., ~3 km NW of Tapia; 700 m, 26°33'54"S, 65°17'22"W; 19.iii.2003; J. Heraty. Will be housed in UCRC.

Description. ***Body length*****:** 3.7 mm. ***Length of forewing*****:** 3.3 mm. ***Length of hind wing*****:** 2.6 mm. ***Head*****.** Antenna relatively thick with 24 flagellomeres; first flagellomere 1.5 × as long as second. Median width of eye 0.3 × longer than median width of gena in lateral view (0.3:0.1). Width of anterior ocellus 0.9 × longer than distance between posterior ocelli (0.08:0.09). Apex of clypeus convex with a smooth apical margin. Maxillary palpus 5-segmented; labial palpus 4-segmented. Occipital carina well developed dorsally, absent ventrally (This may be a pseudo-occipital carina, i.e., secondarily derived, as is found in some Agathidinae, e.g., *Marjoriella* spp.). Most of head with weak microsculpture contrasting sharply with the smooth, glabrous occiput. Malar suture present. Interantennal space with a bicarinate ridge. Median ocellus surrounded medially and laterally by a smooth, curved ridge. ***Mesosoma*****.** Pronotum bilobed anteriorly with a transverse plate dorsally. Notauli deeply impressed and entirely costate. Median lobe of mesoscutum bilobed. Scutellar sulcus deep with a median carina; median width of scutellar sulcus 0.4 mm; median length of scutellar sulcus 0.1 mm; median length of scutellar sulcus 0.1 × longer than median length of mesosoma in dorsal view (0.1:0.9). Scutellum smooth and flat. Postscutellar depression absent. Propleuron lacking a posterolateral lobe. Epicnemial carina strong and complete. Precoxal sulcus well defined with ~5 costulae. Propodeum rugose with a large, well-defined median areola. ***Wings*****.** Forewing M+Cu entirely tubular; 1RS vein long; second submarginal cell large and greatly compressed apically, trapezoid, maximum length of the cell 1.6 × longer than its maximum height

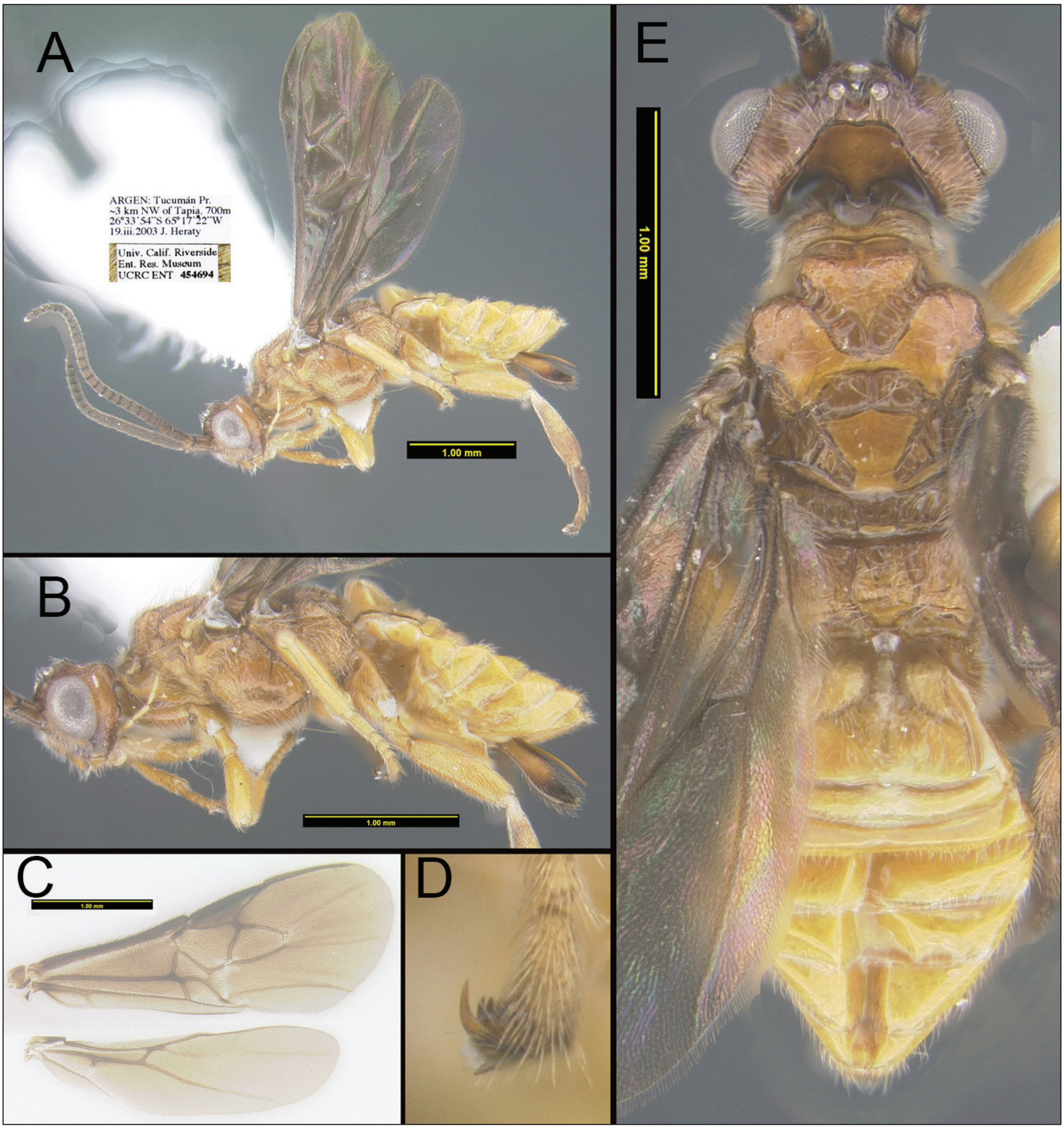


Figure 1. *Dickyyuella argentinensis* Kang & Sharkey, sp. nov. holotype **A** lateral habitus of the specimen, including antennae and wings **B** lateral view, zoomed in on head, mesosoma, and metasoma **C** wings **D** hind tarsal claw **E** dorsal habitus of the specimen, zoomed in on head, mesosoma, and metasoma.

(0.46:0.28); apical abscissa of RS entirely nebulous and almost straight, very slightly curved posteriorly; (RS+M)b about 3 × longer than m-cu vein; 1M about 3 × longer than m-cu vein; anal crossvein indicated by a slight swelling on vein A. Hind wing unremarkable; lacking distinct claval lobe; veins M+Cu and M about equal in length; r crossvein absent. ***Legs.*** Midtibia 3.4 × longer than midbasitarsomere (0.64: 0.19). Hind femur 0.9 × longer than hind tibia (0.75:0.84). Hind basitarsomere swollen. Tarsal claws rather large with pectinate base. ***Metasoma.*** Metasoma 1.1 × longer than mesosoma (1.70:1.56). Spiracle of T1 on membranous laterotergite. T1 0.7 × longer than its apical width (0.63:0.45), with carinate lateral margins; median area of T1 with an inverse Y-shaped depression. Remaining terga smooth and rather weakly sclerotized. T2 transverse, much wider than long. Hypopygium acute apically and not nearly reaching apex of metasoma. Ovipositor sheath about half as long as metasoma, strongly compressed laterally, with fine sparse setae. Ovipositor simple, slightly downcurved but otherwise unmodified. ***Color.*** Head and mesosoma mostly light brown; antenna brown, foreleg and midleg entirely pale, hind tibia and tarsus yellow medially, hind claw brown. Metasoma mostly pale except ovipositor sheath, ovipositor sheath light brown basally, apically dark brown. Wings entirely infuscate.

Male. Unknown.

Biology. Unknown.

Distribution. Neotropics. *Dickyyuella argentinensis* Kang & Sharkey, sp. nov., is known from Tapia, Tucumán Pr., Argentina, near Rio India Muerta.

Etymology. The species is named after the collecting country, “Argentina”.

Taxonomic placement

Dickyyuella Kang & Sharkey, gen. nov., is tentatively placed as a new member of the microgastroid complex. This is based on three synapomorphies, i.e., spiracle of T1 on the laterotergite; spiracle of T7 absent; apical abscissa of forewing vein RS nebulous (not tubular). We had some difficulty placing this species phylogenetically within the microgastroid complex due to the presence of what are usually considered plesiomorphic characters, based on Cheloninae as the outgroup (Whitfield and Mason 1994; Whitfield 1997; Belshaw et al. 1998; Dowton and Austin 1998; Dowton et al. 1998; Dowton et al. 2002; Banks and Whitfield 2006; Murphy et al. 2008; Sharanowski et al. 2011), i.e., complete occipital and epicnemial carinae. Since the occipital and epicnemial carinae are rarely present in the microgastroid complex and partially developed in a few scattered taxa, we consider the condition to be secondarily derived states. The former character state is rarely known in the complex except for a few species of Microgastrinae, e.g., *Philoplitis* Nixon, 1965 (Ranjith et al. 2019). Some cardiochiline members, e.g., *Austerocardiochiles* Dangerfield, Austin & Whitfield, 1999 and *Psilommiscus* Enderlein, 1912, have partially developed occipital carina in the malar region (Fig. 2A). The epicnemial carina is rare, being found in a few Microgastrinae, e.g., *Fornicia* Brullé, 1846 and *Snellenius* Westwood, 1882 some members of Cardiochilinae, e.g., *Austerocardiochiles*, *Bohayella* Belokobylskij, 1987 and *Toxoneuron* Say, 1836 (Fig. 2B), and weaker in *Mendesella* Whitfield & Mason, 1994 of the Mendesellinae (Whitfield, pers. comm. 2021). In Microgastrinae, the condition does not seem to be the ground-plan state for the subfamily. Of the two genera in Mendesellinae, only species of *Mendesella* have an epicnemial carina, so the ground-plan of the subfamily is equivocal. Based on these two apparently plesiomorphic character states, our first impression of the specimen was that it may be a new subfamily, sister to the remaining microgastroids, who possess apomorphic states of these characters.

Closer inspection of the specimen revealed that the first metasomal median tergite has an inverted Y-shaped groove, which is a unique character state within the microgastroids and possessed only by members of Cardiochilinae (Fig. 1E). Further evidence to suggest membership is the pectinate tarsal claws which are found in the majority of cardiochiline genera and are relatively rare in other microgastroids, e.g., a few species of *Apanteles* Föerster, 1863, *Carlmuesebeckius*

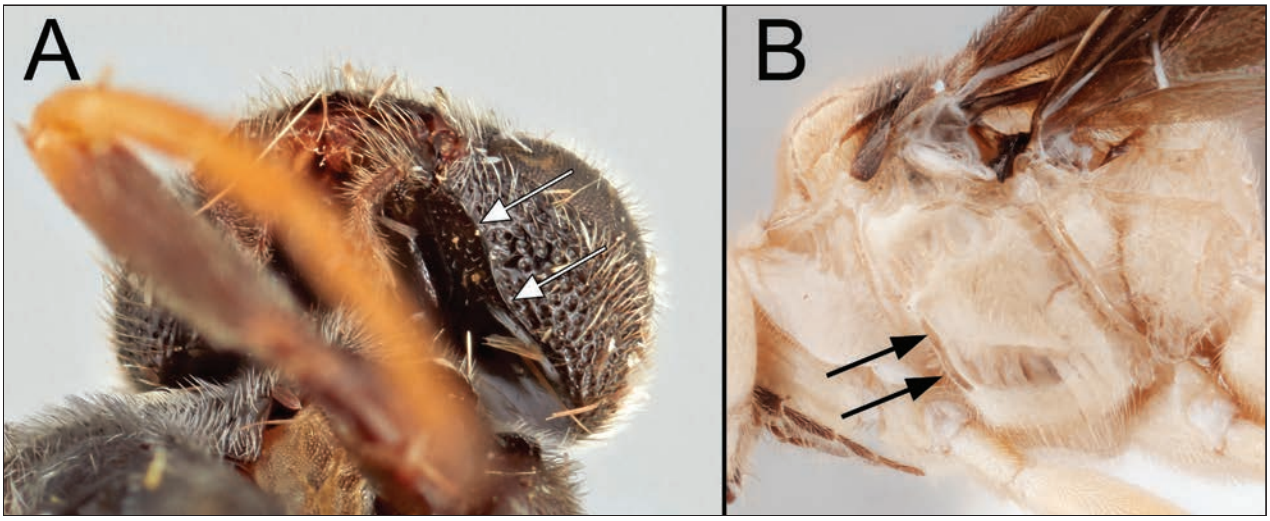


Figure 2. A Posteroventral head of *Austerocardiochiles* sp.; arrows: occipital carina **B** mesopleuron of *Bohayella rodrigodiazi* Kang, 2022; arrows: epicnemial carina.

Fernandez-Triana, 2018, *Ohenri* Fernandez-Triana, 2018 (Fernandez-Triana and Boudreault 2018) (Fig. 1D). The phylogenetic relationships of Cardiochilinae are largely conjecture, despite the best efforts of Dangerfield et al. (1999); therefore, it is unclear if this is ground-plan or derived. Based on these ambiguous phylogenetic cues we favor the Cardiochilinae hypothesis. This implies that the occipital and epicnemial carinae are secondarily derived and there is no reason to believe that *Dickyyuella* Kang & Sharkey, gen. nov. is the sister to all other Cardiochilinae, although there is no evidence to the contrary either.

Acknowledgements

We acknowledge Dr Jim Whitfield for sharing his knowledge on the microgastroid complex with us. We also thank principal museum scientists at UCRC, Drs Douglas Yanega and Serguei Triapitsyn for specimen loans. Lastly, we are grateful to the Department of Entomology, Kyungpook National University for supporting the first author's research in a stable environment.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

Kyungpook National University.

Author contributions

Conceptualization: MJS. Data curation: IK. Formal analysis: IK, MJS. Funding acquisition: IK. Methodology: IK, MJS. Writing - original draft: IK, MJS. Writing - review and editing: IK, MJS.

Author ORCIDs

Ilgoo Kang https://orcid.org/0000-0002-8501-1758
Michael J. Sharkey https://orcid.org/0000-0001-6201-7340

Data availability

All of the data that support the findings of this study are available in the main text.

References

Banks JC, Whitfield JB (2006) Dissecting the ancient rapid radiation of microgastrine wasp genera using additional nuclear genes. Molecular Phylogenetics and Evolution 4(3): 690–703. https://doi.org/10.1016/j.ympev.2006.06.001

Belshaw R, Fitton M, Herniou E, Gimeno C, Quicke DLJ (1998) A phylogenetic reconstruction of the Ichneumonoidea (Hymenoptera) based on the D2 variable region of 28S ribosomal RNA. Systematic Entomology 23(2): 109–123. https://doi.org/10.1046/j.1365-3113.1998.00046.x

Dangerfield PC, Austin AD, Whitfield JB (1999) Systematics of the world genera of Cardiochilinae (Hymenoptera: Braconidae). Invertebrate Systematics 13(6): 917–976. https://doi.org/10.1071/IT98020

Dowton M, Austin AD (1998) Phylogenetic relationships among the microgastroid wasps (Hymenoptera: Braconidae): combined analysis of 16S and 28S rDNA genes and morphological data. Molecular Phylogenetics and Evolution 10(3): 354–366. https://doi.org/10.1006/mpev.1998.0533

Dowton M, Austin AD, Antolin MF (1998) Evolutionary relationships among the Braconidae (Hymenoptera: Ichneumonoidea) inferred from partial 16S rDNA gene sequences. Insect Molecular Biology 7: 129–150. https://doi.org/10.1046/j.1365-2583.1998.72058.x

Dowton M, Belshaw R, Austin AD, Quicke DLJ (2002) Simultaneous molecular and morphological analysis of braconid relationships (Insecta: Hymenoptera: Braconidae) indicates independent mt-tRNA gene inversions within a single wasp family. Journal of Molecular Evolution 54(2): 210–226. https://doi.org/10.1007/s00239-001-0003-3

Fernandez-Triana J, Boudreault C (2018) Seventeen new genera of microgastrine parasitoid wasps (Hymenoptera: Braconidae) from tropical areas of the world. Journal of Hymenoptera Research 64: 25–140. https://doi.org/10.3897/jhr.64.25453

Harris RA (1979) Glossary of surface sculpturing. Occasional Papers in Entomology 28: 1–31. https://doi.org/10.5281/zenodo.26215

Jasso-Martínez JM, Brady SG, Kula RR (2023) Phylogenetic affinities of the non-cyclostome subfamilies Amicrocentrinae and Dirrhopinae (Hymenoptera, Braconidae) confirmed by ultraconserved element data. Journal of Hymenoptera Research 96: 1017–1030. https://doi.org/10.3897/jhr.96.111012

Murphy N, Banks J, Whitfield JB, Austin A (2008) Phylogeny of the parasitic microgastroid subfamilies (Hymenoptera: Braconidae) based on sequence data from seven genes, with an improved time estimate of the origin of the lineage. Molecular Phylogenetics and Evolution 47(1): 378–395. https://doi.org/10.1016/j.ympev.2008.01.022

Quicke DLJ, van Achterberg C (1990) Phylogeny of the subfamilies of the family Braconidae (Hymenoptera). Zoölogische Verhandelingen 258: 1–95. https://doi.org/10.1111/j.1096-0031.1992.tb00068.x

Ranjith AP, Fernandez-Triana J, Veena T, Priyadarsanan DR, Nasser M (2019) Four new species of *Philoplitis* Nixon (Braconidae, Microgastrinae) with an updated key and illustrations of all described species. ZooKeys 841: 125–150. https://doi.org/10.3897/zookeys.841.33549

Sharanowski BJ, Dowling AP, Sharkey MJ (2011) Molecular phylogenetics of Braconidae (Hymenoptera: Ichneumonoidea), based on multiple nuclear genes, and implications for classification. Systematic Entomology 36(3): 549–572. https://doi.org/10.1111/j.1365-3113.2011.00580.x

Sharkey MJ (1993) Family Braconidae. In: Goulet H, Huber JT (Eds) Hymenoptera of the World: An Identification Guide to Families. Research Branch Agriculture Canada Publication, Ottawa, 362–395.

Sharkey MJ, Wharton RA (1997) Morphology and Terminology. In: Wharton RA, Marsh PM, Sharkey MJ (Eds) Manual of the New World Genera of the Family Braconidae (Hymenoptera). Special Publication of The International Society of Hymenopterists, Washington, D.C., 19–37.

Whitfield JB (1997) Molecular and morphological data suggest a common origin for the polydnaviruses among braconid wasps. Naturwissenschaften 34(11): 502–507. https://doi.org/10.1007/s001140050434

Whitfield JB, Mason WRM (1994) Mendesellinae, a new subfamily of braconid wasps (Hymenoptera: Braconidae) with a review of relationships within the microgastroid assemblage. Systematic Entomology 19(1): 61–76. https://doi.org/10.1111/j.1365-3113.1994.tb00579.x

Yu DS, van Achterberg K, Horstmann K (2016) Biological and taxonomical information: Ichneumonoide. Taxapad Interactive Catalogue, Ottawa. Database on flash drive.

ZooKeys 1208: 173–239 (2024)
DOI: 10.3897/zookeys.1208.116083

Research Article

Contributions on a small collection of the former Subulinidae Fischer & Crosse, 1877 (Eupulmonata, Achatinoidea) with catalogue of the *Glessula* and *Rishetia* species recorded from Myanmar

Nem Sian Man[1,2], Jonathan D. Ablett[3], Ngwe Lwin[4], Chirasak Sutcharit[1], Somsak Panha[1,5]

1 *Animal Systematics Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok, 10330, Thailand*
2 *Department of Zoology, University of Yangon, University Avenue Road, Kamayut Township 11041, Yangon, Myanmar*
3 *Department of Life Sciences, The Natural History Museum, Cromwell Road, London SW7 5BD, UK*
4 *Fauna and Flora International, No. 35, 3rd Floor, Shan Gone Condo, Myay Ni Gone Market Street, Sanchaung Township, Yangon, Myanmar*
5 *Academy of Science, The Royal Society of Thailand, Bangkok 10300, Thailand*
Corresponding authors: Chirasak Sutcharit (chirasak.s@chula.ac.th, jirasak4@yahoo.com); Somsak Panha (somsak.pan@chula.ac.th, somsak_panha@yahoo.com)

Abstract

The taxonomy of subulinid snails in Myanmar has been evaluated, resulting in the recognition of 40 species and subspecies across nine genera: *Allopeas*, *Bacillum*, *Curvella*, *Glessula*, *Opeas*, *Paropeas*, *Rishetia*, *Tortaxis*, and *Zootecus*. Nine species are re-described based on recently collected specimens, and two new species, *Glessula mandalayensis* Man & Panha, **sp. nov.** from Mandalay Region and *Tortaxis cylindropsis* Man & Panha, **sp. nov.** from Shan State are introduced. The genitalia and radula of *Zootecus pullus* was studied for the first time. This study also presents a comprehensive list of all subulinid species recorded to date from Myanmar. The type specimens and authenticated museum specimens have been illustrated with accompanying taxonomic remarks and nine species formerly assigned in *Glessula* are now placed in *Rishetia*: *R. akouktoungensis*, *R. baculina*, *R. basseinensis*, *R. burrailensis maxwelli*, *R. kentungensis*, *R. limborgi*, *R. nathiana*, *R. pertenuis*, and *R. pertenuis major*.

Key words: Conservation, molluscs, Southeast Asia, systematics, taxonomy, type specimen

OPEN ACCESS

Academic editor: Menno Schilthuizen
Received: 22 November 2023
Accepted: 12 June 2024
Published: 30 July 2024

ZooBank: https://zoobank.org/0215503D-E8B4-4179-89F6-FB2CCC59F37E

Citation: Man NS, Ablett JD, Lwin N, Sutcharit C, Panha S (2024) Contributions on a small collection of the former Subulinidae Fischer & Crosse, 1877 (Eupulmonata, Achatinoidea) with catalogue of the *Glessula* and *Rishetia* species recorded from Myanmar. ZooKeys 1208: 173–239. https://doi.org/10.3897/zookeys.1208.116083

Table of contents

Introduction

The Subulinidae Fischer & Crosse, 1877 is a highly diverse land snail family comprised of more than 800 species and approximately 80 genera which are native to tropical and subtropical regions in South and Central America, Africa, and South and Southeast Asia (Gude 1914; Naggs 1994; Schileyko 1999; D'ávila et al. 2020; Horsák et al. 2020). In general, subulinid snails are characterised by having a small to medium-sized (6–66 mm in height), ovate to slender, elongated conical shell, a mostly turreted spire, smooth to strong sculptures, and a concave or straight and truncated or continuous columella (Pilsbry 1906; Godwin-Austen 1920; Schileyko 1999; Do and Do 2014). The genitalia consist of a simple and slender to muscular penis, with (sometimes variously developed flagella) or without epiphallus (Gude 1914; Godwin-Austen 1920; Schileyko 1999; Budha 2017; Budha et al. 2017; D'ávila et al. 2018).

The earliest overview of molecular phylogenetic studies of the stylommatophorans revealed the 'achatinoid' clade, which principally comprises the Achatinoidea Swainson, 1840 [including the subulinid snails] and the Streptaxoidea Gray, 1860 (Wade et al. 2001, 2006). It confirms the traditional and widely accepted hypothesis that the Subulinidae belong within the Achatinoidea. However, the systematic classification of the achatinoideans has varied considerably and has been subject to change throughout time. The name 'Subulininae' was initially nominated, and then was subsequently raised to the family level under the 'Achatinacea' [= Achatinoidea] (Fischer and Crosse 1877; Thiele 1931: 549). This classification was later followed by Zilch (1959) and Vaught (1989). At the same time, some studies considered 'subulinids' as a subfamily of the Achatinidae (Inkhavilay et al. 2019; Neubert and Bochud 2020; MolluscaBase 2023). Whereas Schileyko (1999) reclassified the 'subulinids' as its own superfamily consisting of the Subulinidae Glessulidae Godwin-Austen, 1920, Micractaeonidae Schileyko, 1999 and Ferrussaciidae Bourguignat, 1883, and recognised nine subfamilies within the Subulinidae. Recently, the multi-gene phylogeny of the Achatinoidea revealed the (sub)family as classified in Zilch (1959), Vaught (1989) and Schileyko (1999) are polyphyletic (Fontanilla et al. 2017). More recently, Bouchet et al. (2017) treated 'Subulinidae sensu by earlier authors' as a subfamily of the Achatinidae. Additionally, taxonomic placements within the Achatinoidea have also varied substantially since the revisions based on exhaustive anatomical characters had not been provided. Therefore, systematic classification of the Achatinoidea remains a source of discussion but surpasses the scope of this work, which aims to highlight the Subulinidae from Myanmar, as classified in Zilch (1959) and Vaught (1989), and to attract and encourage further systematic research.

The subulinid snails are highly diverse and primarily found in Africa and also in Southeast Asia. In Myanmar, six genera are known: *Bacillum* Theobald, 1870, *Curvella* Chaper, 1885, *Glessula* von Martens, 1860, *Opeas* Albers, 1850, *Prosopeas* Mörch, 1876, and *Zootecus* Westerlund, 1887 with a total of 37 nominal species being documented (Gude 1914; Godwin-Austen 1920). Most of these nominal species have been described based solely on shell morphology, with uncertain taxonomic status and distribution due to the scarcity of detailed illustrations of their respective type specimens and a lack of newly collected samples for over a century since the work of Gude (1914) and Godwin-Austen (1920). Therefore, this work focuses on examining the historical museum specimens, both type and non-type, and also newly collected materials, with the aim to update the taxonomic knowledge of achatinoid snails from Myanmar. Recent specimen collections were conducted in collaboration with the Forest Department of Myanmar and Fauna and Flora International (FFI), as described in our previously published taxa (Man et al. 2022, 2023). This paper will enhance the knowledge of the Subulinidae diversity in Myanmar, contribute to our understanding of land snail biogeography and will serve as a valuable resource for the improvement of the existing taxonomy of the subulinid taxa.

Materials and methods

Sampling and morphological studies

Between 2015 and 2016, malacofauna surveys of the limestone habitats in Myanmar were resumed through collaborative efforts involving the Animal Systematics Research Unit (ASRU), the Forest Department of Natural Resources and Environmental Conservation and Forestry, Myanmar, and Fauna and Flora International (FFI), under the framework of an MOU (Letter No. 0092). During field trips, small samples of subulinid snails were primarily collected in Shan State and the Mandalay Region within the northeastern part of the country, as well as in Kayin and Mon states and the Tanintharyi Region in the southeast, as shown in Fig. 1.

These newly collected samples were deposited in the Chulalongkorn University, Museum of Zoology (**CUMZ**), Thailand. The specimens were examined for shell morphology (Fig. 2) and reproductive system structure (when available), and the terminology used in this study follows Gude (1914), Godwin-Austen (1920), Schileyko (1999), and Budha et al. (2017). Specimens were compared to the type specimens and available authenticated collections. Adult and intact shells were measured with a digital calliper for shell height (**SH**; largest length from the apex to the base of aperture), shell width (**SW**; widest diameter from one side of the last whorl to the outermost side of aperture), and whorl counts (Kerney and Cameron 1979; Table 1).

The following species list was produced using both the literature and collections, the primary type specimens (i.e., holotype, lectotype, syntype(s), and neotype) and secondary type specimens [paratype(s) and paralectotype(s)]. The taxa are arranged in alphabetical order according to their current taxonomic status. The references for the usage of each taxon name are provided herein. The name

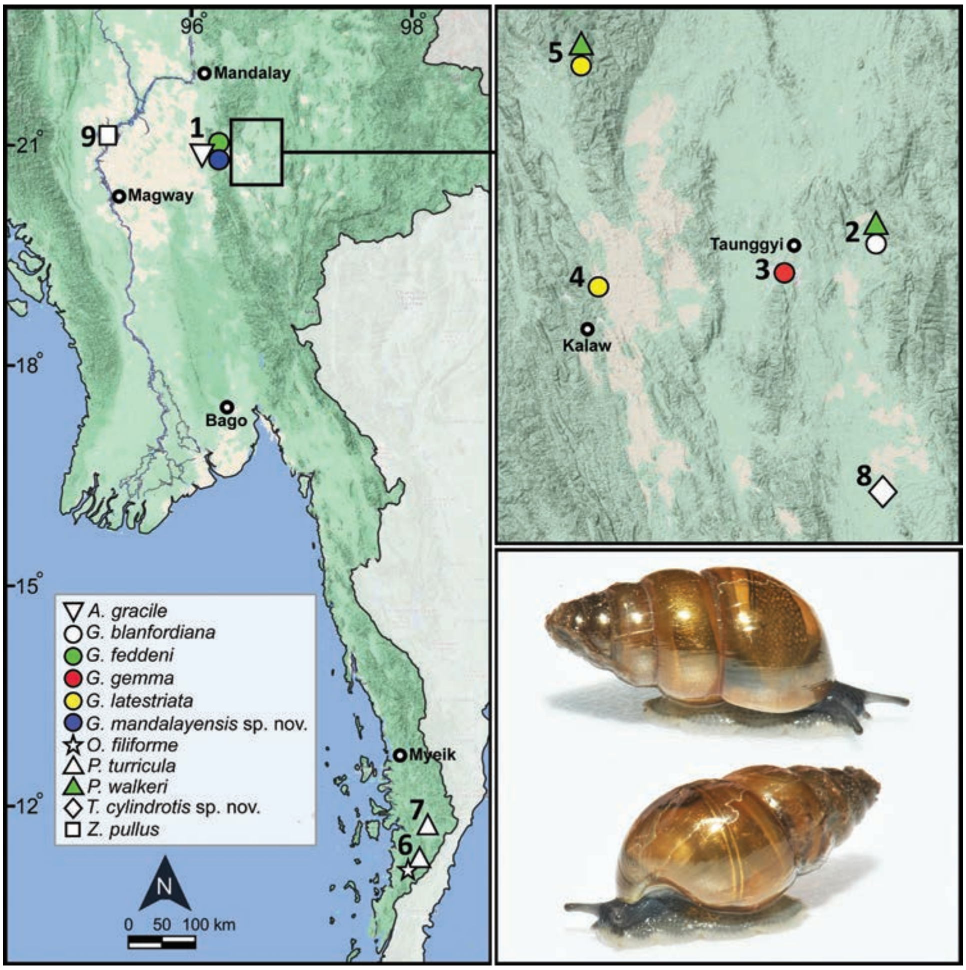


Figure 1. Approximate collecting localities of the subulinids from Myanmar examined in this study (right), inset figure (upper right) indicates the collecting site from Shan State, and living snails (lower right) of *Glessula mandalayensis* sp. nov., paratype CUMZ 13073 from Pyinyaung Village, Mandalay Region, Myanmar (SH ~ 14 mm). The numbers correspond to localities listed in Table 1.

in the original combination is given with bibliographic information on the original description. The type locality is given, and if possible, the modern name and/or regional names of the type locality are provided in square brackets. Where necessary, remarks are given on the status of type specimens, authorships, availability of name, notes on the type locality, and further valuable comments.

Institutional abbreviations

ANSP	Academy of Natural Science of Philadelphia, Drexel University, Philadelphia
B.M.	used in old labels for the British Museum (now The Natural History Museum (NHM), London)
CUMZ	Chulalongkorn University Museum of Zoology, Bangkok
MNHN	Muséum National d'Histoire Naturelle, Paris
NHMUK	The Natural History Museum, London
SM	Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main
UMZC	University Museum of Zoology Cambridge, Cambridge
ZMB	Museum für Naturkunde, Humboldt University, Berlin

Table 1. Shell measurements of subulinid species examined in this study. SH: shell height; SW: shell width. The localities numbers are indicated in Fig. 1.

Species, locality no., and CUMZ no.	No. of specimens	Ranges, mean ± S.D. in mm		SH/SW ratio	No. of whorls
		Shell height	Shell width		
Allopeas gracile					
1. Pyinyaung Village, Meiktila, Mandalay (13066)	8	9.8–12.1 10.76 ± 0.92	2.9–3.3 3.08 ± 0.169	3.37–3.78 3.48 ± 0.17	7½–8
Glessula blanfordiana					
2. Aik Kham Cave, Taunggyi, Shan (13067)	3	7.7–8.6 8.16 ± 0.47	3.7–3.9 3.81 ± 0.08	2.05–2.26 2.141 ± 0.10	6–6½
Glessula feddeni					
1. Pyinyaung Village, Meiktila, Mandalay (13068)	8	7.8–10.8 9.72 ± 1.14	4.0–4.8 4.47 ± 0.33	1.95–2.25 2.16 ± 0.11	6½ –7
Glessula gemma					
3. Montawa Cave, Taunggyi, Shan (13069)	5	8.7–9.2 8.99 ± 0.28	3.4–3.9 3.61 ± 0.22	2.37–2.58 2.49 ± 0.09	6½–7
Glessula latestriata					
4. Thale Cumon Temple, Kalaw City, Shan (13070)	4	8.4–10.8	4.0–4.7	1.86–2.31	6½–7
5. Ywangan Village, near Lin Way Monastery, Kalaw, Shan (13071)		9.22 ± 1.14	4.51 ± 0.18	2.04 ± 0.23	
Glessula mandalayensis sp. nov.					
1. Pyinyaung Village, Meiktila, Mandalay (13072, 13073)	30	13.3–16.0 14.32 ± 0.72	6.7–7.8 7.19 ± 0.30	1.87–2.12 1.99 ± 00.07	6–7
Opeas filiforme					
6. Phra (Buddha) Cave, Tanintharyi (13074)	15	8.1–11.2 9.51 ± 1.00	2.4–3.4 2.82 ± 0.30	3.32–3.49 3.37 ± 0.05	7½–8
Paropeas turricula					
6. Phra (Buddha) Cave, Tanintharyi (13075)	3	11.7–15.0	3.00–3.90	3.78–3.9	8, 8½
7. Lampane Village, Tanintharyi (13076)		13.00 ± 1.72	3.4 ± 0.45	3.84 ± 0.58	
Paropeas walkeri					
2. Aik Kham Cave, Taunggyi, Shan (13077)	5	8.4–15.3	3.3–3.8	2.54–4.02	8–8½
5. Ywangan Village, near Lin Way Monastery, Kalaw, Shan (13078)		12.65 ± 1.76	3.54 ± 0.22	3.54± 0.56	
Tortaxis cylindropsis sp. nov.					
8. Parpant area, Taunggyi, Shan (13079, 13080)	35	9.3–11.7 10.29 ± 1.06	2.1–2.5 2.27± 0.16	4.11–5.00 4.53 ± 0.39	8–9½
Zootecus pullus					
9. Dhammayazaka Pagoda, Bagan, Mandalay (13081, 13082)	90	11.2–13.3 11.99 ± 0.75	4.3–4.8 4.55 ± 0.16	2.48–2.80 2.63 ±0.14	8–9½

Systematic account

Family Subulinidae Fischer & Crosse, 1877

Genus *Allopeas* Baker, 1935

Lamellaxis (*Allopeas*) Baker, 1935: 84. Zilch 1959: 349.
Allopeas—Schileyko 1999: 509.

Type species. *Bulimus gracilis* Hutton, 1834, by original designation.

Diagnosis. Shell slender and conical; spire high and gradually attenuated; embryonic whorls pointed and smooth; subsequent whorls with striations.

Aperture vertical, broad, and oblong; columella straight, and columellar margin expanded near umbilicus. Penis long, fusiform shape at base then narrowing towards epiphallus, and flagellum absent; vagina cylindrical and narrow tube, and ~ 1/2 of penis length.

Remarks. The genus is sometimes confused with *Paropeas* Pilsbry, 1906 and *Opeas* Albers, 1850. *Allopeas* can be distinguished from *Paropeas* by its less turreted shell, finner striations, smooth embryonic whorls, straight columella, and columellar margin expanded (Table 2). *Paropeas* possesses a mostly turreted shell, stronger irregular striations throughout and entire whorls, concave columella, and columellar margin less expanded. Additionally, *Allopeas* can be differentiated from *Opeas* by having larger and broader shell, attenuated spire, and stronger striations (Schileyko 1999). By contrast, *Opeas* has a smaller and narrower shell, cylindrical or less attenuated spire, and finer striations (Pilsbry 1906).

The genus *Allopeas* consists of ~ 25 species distributed across tropical regions of Asia, Europe, Africa, and America (Schileyko 1999; MolluscaBase 2023). In Southeast Asia, Vietnam has recorded four species (Schileyko 2011), while Cambodia, Laos, Myanmar, and Thailand have reported only one species, namely *Allopeas gracile* (Gude 1914; Inkhavilay et al. 2019; Sutcharit et al. 2020b).

Table 2. Comparison of shell morphology among subulinid genera recorded in Myanmar. The superscript numbers are references; [1] = Pilsbry (1906), [2] = Gude (1914), [3] = Godwin-Austen (1920), [4] = Naggs (1994), [5] = Schileyko (1999), and [6] = Budha et al. (2017).

Genus (type species)	Shell shape	Spire	Sculpture		Aperture shape	Columella
			Embryonic whorl	Spire whorl		
Allopeas **(*Bulimus gracilis* Hutton, 1834)**[5]	slender conical	high and gradually attenuated	smooth	striations	vertically broad; oblong	straight
Bacillum **(*Achatina cassiaca* Reeve, 1849)**[1]	slender conical	high, turreted, and gradually attenuated	striations	obliqued striations or ribs	obliquely narrow; ovate	concave and truncated
Curvella **(*Curvella sulcata* Chaper, 1885)**[1,5]	oblong-conical	low or high conical and rapidly attenuated	smooth	equally or irregularly spaced striations or ribs	vertically broad; ovate; oblong	straight
Glessula **(*Achatina gemma* Reeve, 1850)**[3,6]	ovate-conical	low conical, and gradually attenuated	smooth or striations	equally spaced of striations; grooves; radial ribs	obliquely narrow or broad; ovate	concave and truncated
Rishetia **(*Achatina tenuispira* Benson, 1836)**[3,6]	slender conical	high, turreted, and gradually attenuated	smooth or striations	equally or irregularly spaced striations or ribs	obliquely, narrow; ovate	concave and truncated
Opeas **(*Helix goodallii* Miller, 1822)**[1,5]	slender conical	low or high, turreted, and gradually attenuated	smooth	smooth; fine striations and growth lines	vertically narrow; oblong	concave or straight
Paropeas **(*Bulimus acutissimus* Mousson, 1857)**[1,2,4]	slender conical	high, turreted, and gradually attenuated	striations	irregular, dense, fine or coarse striations	obliquely narrow or broad; ovate	concave or straight
Tortaxis **(*Achatina erecta* Benson, 1842)**[1]	cylindrical to slender conical	high, mostly turreted, narrowly or cylindrically attenuated	smooth	striations and growth lines	vertically narrow; oblong	concave or straight and with spiral fold below
Zootecus **(*Pupa insularis* Ehrenberg, 1831)**[5]	pupiform	high, broad, and cylindrical	smooth	irregular, dense, fine or coarse striations	obliquely broad; oblong; rounded	straight

1 *Allopeas gracile* (Hutton, 1834)

Fig. 3A–D, Table 1

Bulimus (?) *gracilis* (?) Hutton, 1834: 84, 85, 93. Type locality: Mirzapoor, Futtehpoor Sikra, between Agra and Neemuch [Uttar Pradesh and Madhya Pradesh states, India].
Bulimus (*Opeas*) *gracilis*—Pfeiffer 1856: 156.
Stenogyra (*Opeas*) *gracilis*—von Martens 1860: 265. Pfeiffer and Clessin 1881: 321.
Spiraxis gracilis—Blanford 1861: 362.
Stenogyra gracilis—de Morgan 1885: 389, 390.
Opeas gracilis—Theobald 1878: 146. Godwin-Austen 1895: 443.
Opeas gracile—von Möllendorff 1894: 151. Pilsbry 1906: 125–132, pl. 18, figs 3–6. Gude 1914: 355–357. van Benthem Jutting 1952: 378–380.
Lamellaxis gracilis—van Benthem Jutting 1959: 131, 132.
Lamellaxis (*Allopeas*) *gracile*—Solem 1966: 94.
Allopeas gracilis—Maassen 2001: 81, 82.
Allopeas gracile—Schileyko 2011: 9. Do and Do 2014: 452, fig. 1a. Raheem et al. 2014: 117, 118, fig. 73d–f. Inkhavilay et al. 2019: 50, fig. 21a–c. Sutcharit et al. 2020b: 19.

Type specimens. ***Lectotype*** NHMUK 1856.9.15.68/1 (Fig. 3A) ex. Hutton collection from Mirzapore, designated in Raheem et al. (2014: 118). ***Paralectotypes*** NHMUK 1856.9.15.68/2–11 (10 shells; Fig. 3B).

Other material. Limestone hills (Apache Cement Factory), Pyinyaung Village, Meiktila District, Mandalay Region, Myanmar (20°49'39.1"N, 96°23'35.1"E): CUMZ 13066 (8 shells; Fig. 3C, D).

Description. Shell conically elongated, narrow, translucent, glossy, pale yellowish colour, and with 7½–8 whorls. Apex blunt; protoconch ~ 2 whorls and smooth; subsequent whorls with obliquely more or less fine and crowded riblets. Spire gradually tapering; whorls flatly convex; suture wide and shallow; last whorl largest. Aperture high and oblong shape; peristome thin and columellar margin near umbilicus is little expanded; columella straight. Umbilicus narrowly opened.

Distribution. *Allopeas gracile* is distributed worldwide in America, Africa, Europe, and Asia (Gude 1914; Horsák et al. 2020). In South Asia, it has been reported from India, Pakistan, Sri Lanka, Nepal, and all countries in Southeast Asia (van Benthem Jutting 1952; Panha 1998; Schileyko 2011; Do and Do 2014; Raheem et al. 2014; Budha et al. 2015; Foon et al. 2017; Inkhavilay et al. 2019; Nurinsiyah and Hausdorf 2019; Sutcharit et al. 2020b).

This species was previously reported in Myanmar from several localities, including Kayin State, Mon State, Kachin State, Rakhine State, Yangon Region, and Bago Region (see Gude 1914) and presently in the Mandalay Region.

Remarks. Our material from the Mandalay Region matches well with the type specimen of this species. *Allopeas gracile* is a globally distributed alien species introduced to numerous countries and exhibits significant variability in both size and shape, influenced by its expansive distribution range. This species is commonly found in public parks, irrigation areas, greenhouse environments, and residential campuses (Pilsbry 1906; Neubert and Bochud 2020; Kalita 2022).

Genus *Bacillum* Theobald, 1870

Achatina (*Bacillum*) Theobald in Hanley and Theobald 1870: 17.
Bacillum—Pilsbry 1906: 1. Gude 1914: 343. Godwin-Austen 1920: 7. Zilch 1959: 346. Schileyko 1999: 534.

Type species. *Achatina cassiaca* Reeve, 1849a, subsequent designation by Pilsbry (1906: 1).

Diagnosis. Shell slender and conical in shape; spire high, turreted, and gradually attenuated; embryonic whorls cylindrically rounded, and with or without radial striations; subsequent whorls with equally spaced thick or fine radial striations. Aperture oblique and narrowly ovate; columella concave and truncated, and columellar margin simple or slightly expanded.

Remarks. *Bacillum* can be differentiated from *Allopeas* in being cylindrically rounded and with striations on the embryonic whorls, whilst the columella is concave and truncated (Pilsbry 1906; Schileyko 1999). While *Allopeas* has a narrowly attenuated and smooth embryonic whorls, columella straight, and columellar margin near umbilicus expanded (Table 2).

At present, this genus contains seven species mainly distributed in India, and among these, two species are known from Myanmar (Blanford 1869; Pilsbry 1906; Gude 1914; Ramakrishna et al. 2010; MolluscaBase 2023). All *Bacillum* species are known only from shell morphology, and none of the reproductive anatomy has been published so far. Godwin-Austen (1920) stated, '…extended knowledge of the animals of *Bacillum* and *Glessula* shows that the two genera come next each other…', which suggests Godwin-Austen had dissected *Bacillum*, but his findings were never published.

2 *Bacillum obtusum* (Blanford, 1869)
Fig. 3E–H

Achatina (*Glessula*) *obtusa* Blanford, 1869: 449. Type locality: Bhamo in regno Avae [Bhamo District, Kachin State, Myanmar].
Achatina (*Bacillum*) *obtusa*—Hanley and Theobald 1870: 17, pl. 36, fig. 6.
Achatina obtusa—Pfeiffer 1876: 290.
Glessula obtusa—Nevill 1877: 25.
Stenogyra (*Subulina*) *obtusa*—Pfeiffer and Clessin 1881: 327.
Bacillum obtusum—Pilsbry 1906: 1, 2, pl. 1, fig. 1. Gude 1914: 347.

Type specimens. ***Syntypes*** NHMUK 1906.2.2.349 [re-registered in error as 19850143] (4 shells; Fig. 3E, F) ex. Blanford collection from Bhamo, Upper Burmah.

Other material. NHMUK 1903.7.1.1725 (2 shells + 1 juvenile; Fig. 3G, H) ex. Godwin-Austen collection from Bhamo, Upper Burma. NHMUK 18/88.12.4.1012–1014 (3 shells) from Bhamo. NHMUK (1 shell) ex. TV Oldham collection from Bhamo, Burma. SMF 145947/2 (2 shells) ex. von Möllendorff collection from Bhamo.

Diagnosis. Shell slender, elongate turreted and apical whorls rapidly attenuated; apex rounded, blunt and very large embryonic shell; subsequent whorls with fine radial striae. Suture shallow and whorls flattened. Aperture obliquely subovate; columella curved and truncated.

Distribution. This species is known only from the type locality.

Remarks. No new material of this species was collected in this study, but the syntypes are illustrated for the first time.

3 *Bacillum theobaldi* (Hanley, 1870)

Fig. 3I

Achatina (*Electra*) *theobaldi* Hanley in Hanley and Theobald 1870: 9, pl. 17, fig. 5. Type locality: Near the Salwen [near Salween River, Myanmar].

Achatina (*Glessula*) *theobaldiana* [sic]—Theobald 1870: 395.

Achatina theobaldi—Pfeiffer 1876: 290.

Stenogyra (*Glessula*) *theobaldiana*—Nevill 1878: 172.

Stenogyra (*Subulina*) *theobaldi*—Pfeiffer and Clessin 1881: 327.

Bacillum theobaldi—Pilsbry 1906: 4, pl. 1, fig. 8. Gude 1914: 344, 345. Ramakrishna et al. 2010: 150.

Other material. NHMUK 1912.4.16.121 (1 shell; Fig. 3G) ex. Beddome collection from Burmah.

Diagnosis. Shell elongate turreted and gradually attenuated; apex rounded, blunt and very large embryonic shell; subsequent whorls with strong and equally spaced radial ribs throughout. Aperture ovate; columella curved and truncated.

Distribution. This species was recorded from near the Salween River and in Shan State, Myanmar (Hanley and Theobald 1870; Pilsbry 1906). The additional report from 'India' by Ramakrishna et al. (2010) is possibly erroneous.

Remarks. No new material of this species was examined. *Bacillum theobaldi* was initially proposed without a proper description other than comparing it with *B. cassiacum* (Reeve, 1849a) and with an imprecise type locality noted as 'Near the Salwen' (Hanley and Theobald 1870). Pilsbry (1906) confined the type locality as near to the Salween River in Shan State.

This species is superficially similar to *B. obtusum* in shell shape. However, B. *theobaldi* has equally spaced radial ridges (Fig. 3I), whereas *B. obtusum* processes finer radial striations (Fig. 3H).

Genus *Curvella* Chaper, 1885

Bulimus (*Hapalus*) Albers, 1850: 140. [non Illiger 1801 (Coleoptera)]. Type species Bulimus grateloupi Pfeiffer, 1846. Albers 1860: 238.

Curvella—Chaper, 1885: 49. Pilsbry 1906: 46. Gude 1914: 348. Zilch 1959: 351. Schileyko 1999: 515. Budha et at. 2017: 120.

Type species. *Curvella sulcata* Chaper, 1885, by original designation in Chaper (1885: 48).

Diagnosis. Shell oblong-conical; spire low or high and rapidly attenuated; embryonic whorls smooth; subsequent whorls with equally or irregularly spaced thick or fine radial striations or ribs. Aperture vertical, broad-ovate, or oblong, and somewhat pointed above; columella straight; columellar margin expanded near umbilicus. Penis simple and short papillate or short tube; epiphallus and flagellum absent; vagina large, muscular, and nearly equal to penis length.

Remarks. *Curvella* is clearly distinct from other subulinid genera such as *Allopeas*, *Bacillum*, and *Opeas* by its oblong-conical shell, short spire, high and wide aperture, and its much broader last whorls (Table 2). Regarding the genitalia, this genus displays a more rounded, muscular, short penis and a thicker vagina than *Allopeas* and *Opeas* (Schileyko 1999). In comparison, the two latter genera have a slender, narrow, more elongated penis and vagina compared to *Curvella* (Schileyko 1999; Budha 2017). However, only genitalia of *Curvella sikkimensis* (Reeve, 1850) is known for this genus at present (Budha 2017).

This genus is widely distributed from Africa to South Asia and China, and ~ 95 species have been reported (Pilsbry 1906; Gude 1914; Schileyko 1999; Ramakrishna et al. 2010; Budha et al. 2017; MolluscaBase 2023). There are scattered reports of four *Curvella* species in Myanmar, while one species, *C. tonkiniana* Jaeckel, 1950, has been reported in Vietnam and one species, *C. jousseaumei* (de Morgan, 1885), from Peninsular Malaysia (Gude 1914; Maassen 2001; Schileyko 2011; Vermeulen et al. 2015).

4 *Curvella plicifera* (Blanford, 1865)

Fig. 4A

Bulimus plicifer Blanford, 1865: 77. Type locality: Thayet Myo, Pegu. Pfeiffer 1868: 151. Hanley and Theobald 1874: 34, pl. 80, fig. 8.
Bulimina (*Hapalus*) *plicifera*—Pfeiffer and Clessin 1881: 300.
Buliminus (?) *plicifer*—Kobelt 1901: 688, 689, pl. 103, fig. 22.
Curvella plicifera—Pilsbry 1906: 63, pl. 9, fig. 45. Gude 1914: 352.

Type specimens. ***Syntypes*** NHMUK 1906.2.2.235 (2 shells; Fig. 4A) ex. Blanford collection from Thyetmyo, Pegu? Akouktoung.

Diagnosis. Shell ovate conic; spire low; apex bluntly obtuse; subsequent whorls with prominent growth lines throughout. Suture shallow and whorls flattened. Aperture broadly ovate and somewhat pointed posteriorly; columella straight and expanded; parietal callus thin and with small parietal lamella. Umbilicus narrow.

Distribution. This species is restricted to Myanmar and is known only from the type locality.

Remarks. No new material of this species was found in this study, and only the available syntypes are examined here. The modern name of the type locality is Thayet District, Magway Region, central Myanmar [not in the Bago Region].

Among the four *Curvella* species from Myanmar, this species is similar to *C. pusilla* (Blanford, 1865) in shell shape. However, *C. plicifera* has a small parietal tooth, straight columella, and narrowly opened umbilicus, whereas *C. pusilla* possesses a smooth parietal wall (without tooth), slightly twisted columella plait, and closed umbilicus. Further confirmation from additional specimens is necessary to verify their distinctions.

5 *Curvella pusilla* (Blanford, 1865)
Fig. 4B, C

Spiraxis pusilla Blanford, 1865: 78. Type locality: Prome district, Pegu [Pyay District, Bago Region, Myanmar]. Pfeiffer 1868: 192. Hanley and Theobald 1874: 34, pl. 79, fig. 8.
Hapalus pusillus—Nevill 1878: 174.
Stenogyra [*Spraxis* (*Euspiraxis*)] *pusilla*—Pfeiffer and Clessin 1881: 324.
Curvella pusilla—Pilsbry 1906: 64, pl. 9, fig. 48. Gude 1914: 351.

Type specimens. *Possible syntypes* NHMUK 1906.2.2.234 (2 shells; Fig. 4B) ex. Blanford collection from Akouktong, Pegu.

Other material. NHMUK 1888.12.4.1003–1004 (1 shell identified as *C. pusilla*; Fig. 4C [another shell identified as *C. puta*]) ex. W. Theobald collection from Pegu.

Diagnosis. Shell ovate conic; spire low; apex bluntly obtuse; subsequent whorls with prominent growth lines. Suture shallow and whorls slightly flattened. Aperture broadly ovate and pointed posteriorly; columella twisted and expanded; parietal callus thin. Umbilicus closed.

Distribution. This species seems restricted to Myanmar and is known only from the type locality. The modern administrations of the type locality are 'Prome district' [Pyay District] and 'Pegu' [Bago Region].

Remarks. No new material of this species was found in this study, and only the probable syntypes were examined. These are considered possible syntype material since the locality data (Akouktong, Pegu) does not precisely match that which was given in the original description (Prome district, Pegu).

Blanford (1865) noted that *C. pusilla* resembles the young specimen of *C. puta* (Benson, 1857), but this species has a closed umbilicus, while *C. puta* possesses an opened umbilicus. We recognise *C. pusilla* as a valid species following Blanford's description, and no new materials of this species were examined in this study.

6 *Curvella puta* (Benson, 1857)
Fig. 4D, E

Bulimus putus Benson, 1857: 330. Type locality: Tavoy [Dawei, Tanintharyi Region, Myanmar]. Pfeiffer 1859: 502. Blanford 1865: 94. Hanley and Theobald 1874: 34, pl. 80, fig. 9.
Hapalus putus—Nevill 1878: 178.
Bulimina (*Hapalus*) *puta*—Pfeiffer and Clessin 1881: 299.
Buliminus (?) *putus*—Kobelt 1901: 689, pl. 103, fig. 23.
Curvella puta—Pilsbry 1906: 63, 64, pl. 9, fig. 46. Gude 1914: 351, 352. Preece et al. 2022: 130, fig. 55f.

Type specimen. *Holotype* UMZC I.102795 (Fig. 4D; after Preece et al. 2022: fig. 55f) ex. R. McAndrew ex. Benson collection from Tavoy, Birmah.

Other material. NHMUK 1888.12.4.1003–1004 (1 shell identified as *C. puta*; Fig. 4E [another shell identified as *C. pusilla*]) ex. W. Theobald collection from Pegu. NHMUK 1906.1.1.1033 (1 shell) ex. Godwin-Austen collection from Bassein, Pegu.

Diagnosis. Shell conical; spire high; apex obtuse; subsequent whorls with strong and prominent growth lines. Suture impressed and whorl**s** slightly convex. Aperture semi-ovate and somewhat pointed above; columella straight and dilate; parietal callus thin. Umbilicus narrow.

Distribution. This species was reported from the Tanintharyi and Bago regions of Myanmar and Thailand (Blanford 1865; Gude 1914; Panha 1998).

Remarks. *Curvella puta* was described based on a single bleached specimen collected from 'Tavoy' in Myanmar. No new material of this species was found during this survey, but the type specimens and authenticated museum specimens are illustrated herein.

There is a mixed-species lot, NHMUK 1888.12.4.1003–1004, ex. the W. Theobald collection, labelled '*Hapalus putus* Benson' from 'Pegu', consisting of two shells. The first shell (Fig. 4E) has a high, turreted, and pointed spire, narrowly opened umbilicus, and strong radial striations, which agree with the holotype of *C. puta* from 'Tavoy' (Fig. 4D). The other shell (Fig. 4C) has a lower and convex spire, fine radial striations, narrowly opened umbilicus, and without a parietal tooth, which more resembles *C. pusilla*. In comparison, *C. pusilla* possesses a closed umbilicus without a parietal tooth (Fig. 4B), while *C. plicifera* has an open umbilicus and a small parietal tooth (Fig. 4A).

This mixed-species lot suggests several interpretations: i) an extended distribution of *C. puta* beyond its type locality to the Bago Region in central Myanmar, and ii) the presence or absence of a parietal tooth and an open or closed umbilicus are possibly intraspecific variation rather than diagnostic characters distinguishing between *C. plicifera* and *C. pusilla*. Additional evidence and further specimens from a wider geographic range will clarify this issue.

7 *Curvella scrobiculata* (Blanford, 1865)

Fig. 4F

Bulimus scrobiculatus Blanford, 1865: 77. Type locality: Pegu, west of Irawady [Bago Region, west of Ayeyarwady River, Myanmar]. Pfeiffer 1868: 151. Hanley and Theobald 1874: 34, pl. 79, fig. 9.
Bulimina (*Hapalus*) *scrobiculata*—Pfeiffer and Clessin 1881: 300.
Hapalus scrobiculatus—Nevill 1878: 175.
Curvella scrobiculata—Pilsbry 1906: 64, 65, pl. 9, fig. 49.
Curvella scrobiculatus—Gude 1914: 350, 351.

Type specimens. ***Possible syntypes*** NHMUK 1906.2.2.226 (2 shells; Fig. 4F) ex. Blanford collection from Akouktong, Pegu.

Diagnosis. Shell conical; spire high; apex obtuse; subsequent whorls with strong and equally spaced radial ridges throughout. Suture impressed and whorls flattened convex. Aperture truncate and somewhat pointed posteriorly; columella straight and thickened; parietal callus thin. Umbilicus narrowly open.

Distribution. This species is known only from the type locality and is probably an endemic species in Myanmar.

Remarks. No new material of this species was found in this study, and the probably syntype is illustrated here for the first time. Blanford (1865) described three *Curvella* species, *C. plicifera*, *C. pusilla*, and *C. scrobiculata*, from Myanmar

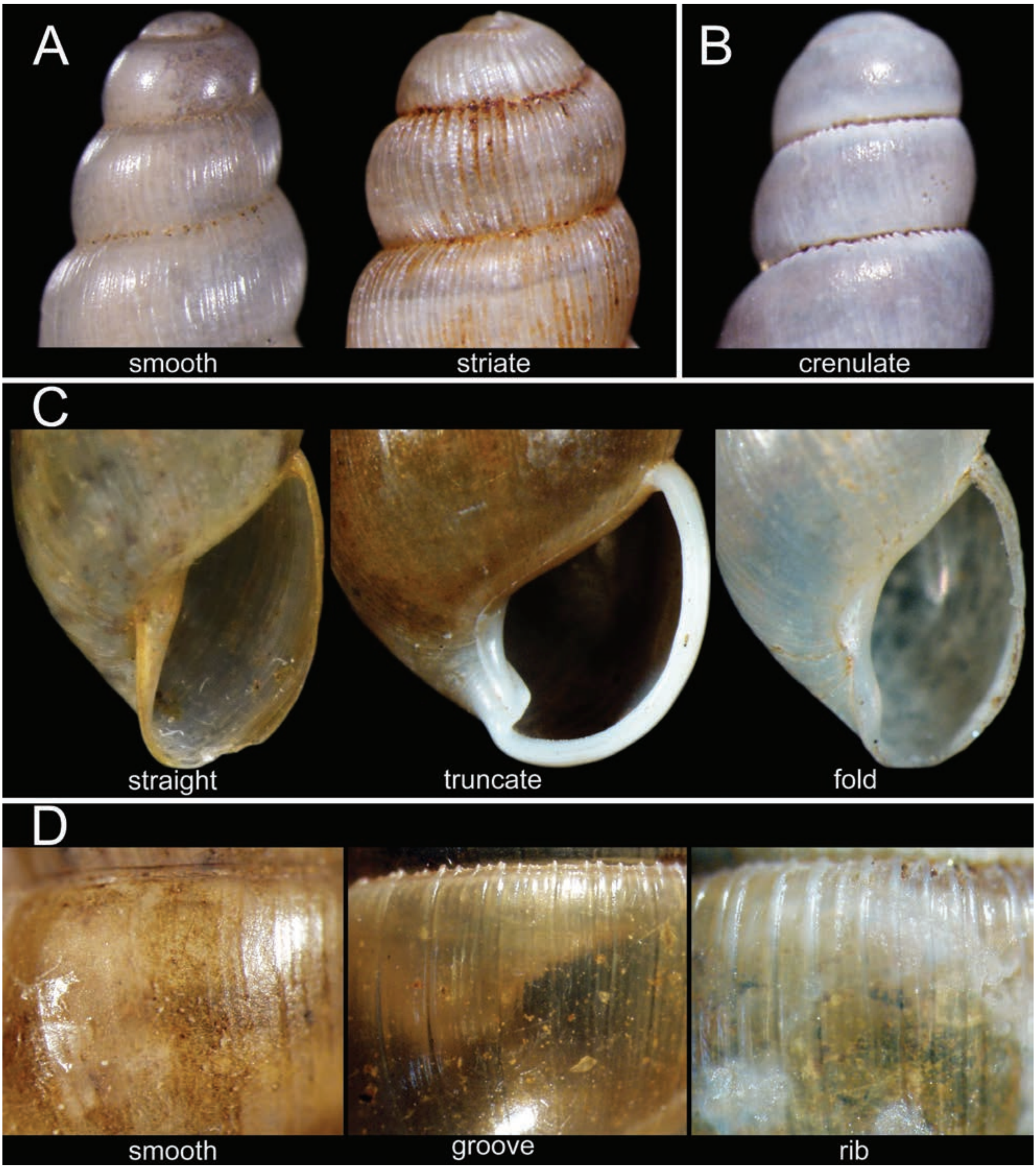


Figure 2. Schematic shell morphology of the subulinid snails **A** protoconch sculptures as recognised in this study: smooth and striate **B** crenulate suture **C** columella shape as recognised in this study: straight, truncate and fold **D** shell surface sculpture of the *Glessula* as recognised in this study: smooth, groove, and ribbed.

consecutively in the same publication with their type localities as 'Pegu' [now in the Bago Region]. Compared to the authenticated museum specimens, *C. scrobiculata* is distinct from *C. puta* by having strong radial ribs, flatter whorls, and a more turreted, pointed, and higher spire. Furthermore, *C. scrobiculata* is easily distinguishable from *C. plicifera* and *C. pusilla* by its higher, pointed, turreted spire and prominent radial ribs. In contrast, the two latter species exhibit

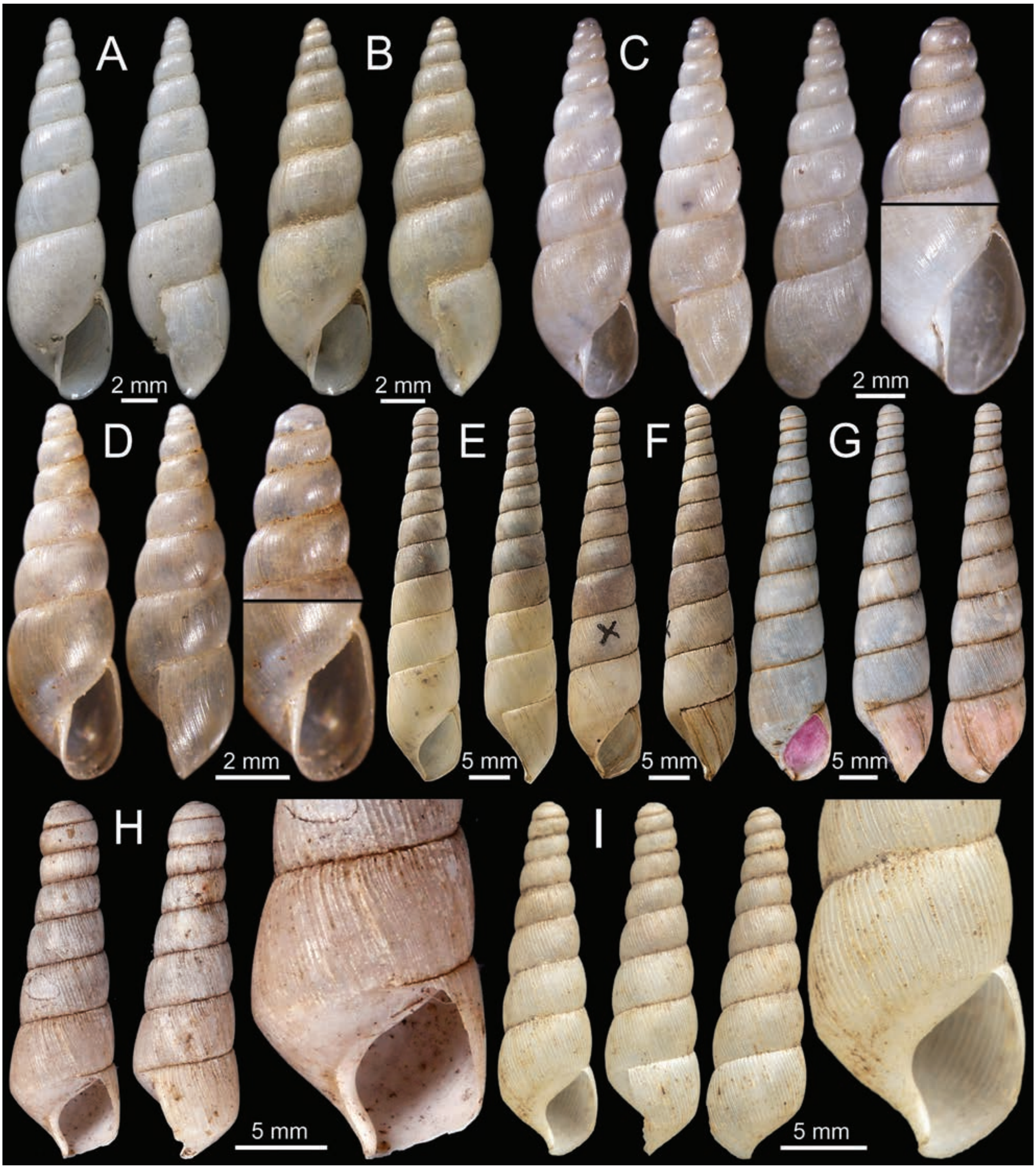


Figure 3. A–D *Allopeas gracile* **A** lectotype NHMUK 1856.09.15.68/1 from Mirzapore **B** paralectotypes NHMUK 1856.09.15.68/2–11 and **C, D** specimen CUMZ 13066 from Mandalay Region, Myanmar with embryonic whorls and aperture **E–H** *Bacillum obtusum* **E, F** syntype NHMUK 1906.2.2.349 from Bhamo, Upper Burmah **G, H** specimen NHMUK 1903.7.1.1725 from Bhamo, Upper Burma and **H** juvenile shell with last whorl **I** *Bacillum theobaldi*, syntype NHMUK 1912.4.16.121 from Burmah with last whorl.

a lower and more convex spire with finer radial striations to nearly smooth shell surfaces. These are considered possible syntype material since the locality data (Akouktong, Pegu) does not exactly match that which was given in the original description (Pegu, west of Irawady).

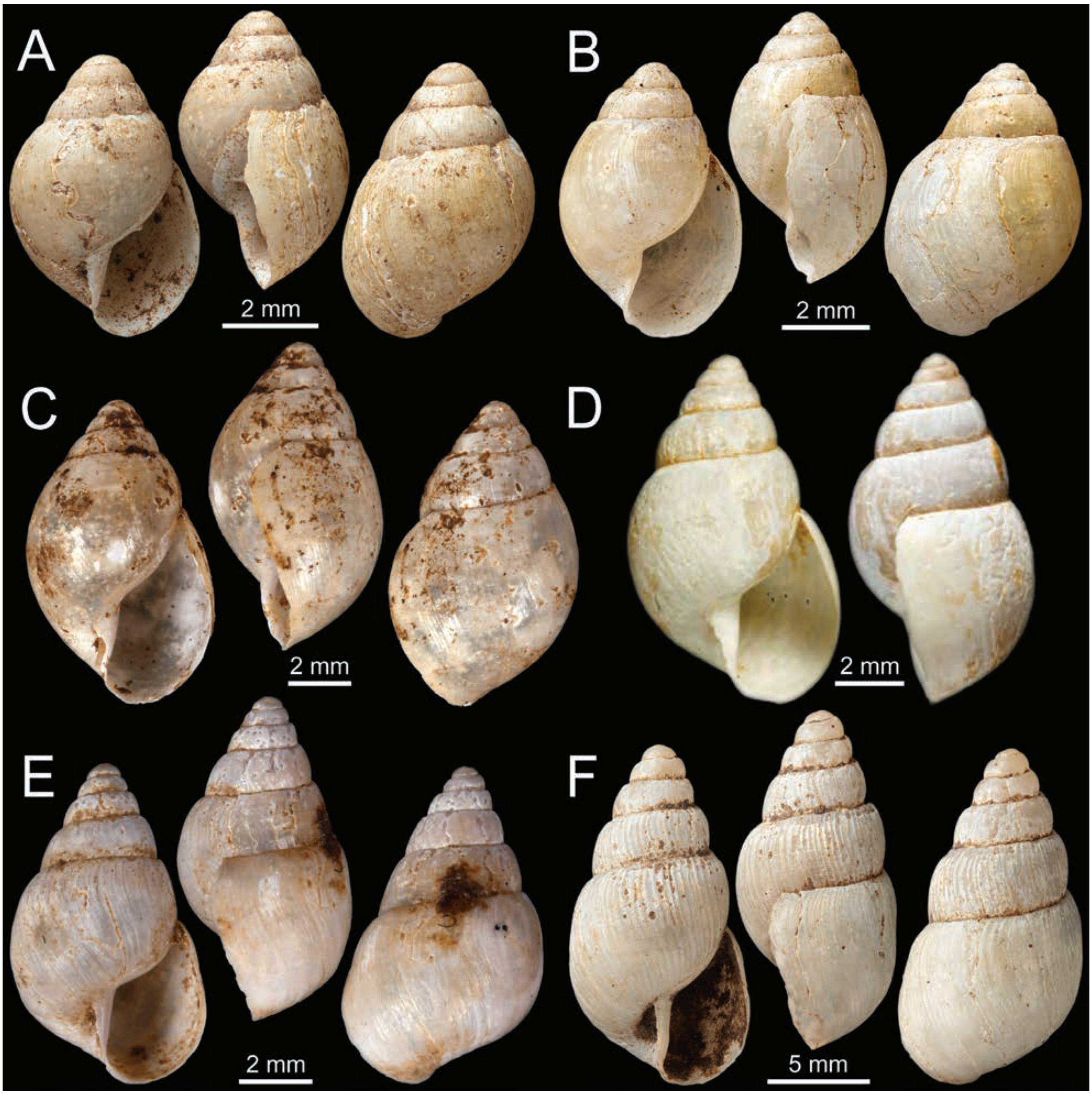


Figure 4. A *Curvella plicifera*, possible syntype NHMUK 1906.2.2.235 from Thyetmyo, Pegu; Akouktoung **B, C** *Curvella pusilla* **B** possible syntype NHMUK 1906.2.2.234 from Akouktong, Pegu and **C** specimen NHMUK 1888.12.4.1003–1004 from Pegu **D, E** *Curvella puta* **D** holotype UMZC I.102795 from Tavoy, Birmah (after Preece et al. 2022: fig. 55f) and **E** specimen NHMUK 1888.12.4.1003–1004 from Pegu **F** *Curvella scrobiculata*, possible syntype NHMUK 1906.2.2.226 from Akouktong, Pegu.

Genus *Glessula* von Martens, 1860

Electra Albers, 1850: 194. [non Lamouroux 1816 (Bryozoa)]. Type species: *Achatina ceylanica* Pfeiffer, 1845. Adams and Adams 1855: 105. Pfeiffer 1856: 168.

Cionella (*Glessula*)—von Martens in Albers 1860: 254. Pfeiffer and Clessin 1881: 329.

Stenogyra (*Glessula*)—Nevill 1878: 166.

Glessula—Tenison-Woods 1888: 1053. Beddome 1906: 160. Pilsbry 1908: 50. Gude 1914: 377. Zilch 1959: 343. van Benthem Jutting 1952: 373, 374. Schileyko 2011: 11.

Type species. *Achatina gemma* Reeve, 1850 by original designation.

Diagnosis. Shell ovate-conical in shape; spire low or high conical, and regularly attenuated; embryonic whorls smooth or with striations; subsequent whorls with equally or irregularly spaced radial striations or ribs. Aperture oblique, narrow to wide, and ovate; columella concave and truncated, and columellar margin not expanded. Penis large, thick, and moderately long; epiphallus short, stout, terminally pointed, and curved; flagellum present (rarely absent) with comb-like or hand-like structures; epiphallic caecum absent; vagina muscularly and nearly equal to ~ 1/5–2/5 of penis length.

Remarks. Superficially, *Glessula* and *Rishetia* are similar in having a concave and truncated columella, but they differ in their shell shape and genital structure (Godwin-Austen 1920; Raheem et al. 2014; Budha et al. 2017). In terms of shell morphology, *Glessula* can be differentiated by its ovate-conical shape, short spire, large and blunt embryonic whorls, while *Rishetia* possesses a slender, conical-shaped elongate spire which narrow and rather acute embryonic whorls (Table 2). Regarding the genital characters, *Rishetia* exhibits a simple, tubular-shaped flagellum with the epiphallic caecum present (Table 3), while *Glessula* displays a well-developed comb-like flagellum (appendage) and the epiphallic caecum absent (Budha et al. 2017); except *G. mandalayensis* sp. nov. which has no flagellum. Likewise, *Glessula* is also distinct from *Curvella* by its concave and truncated columella, not expanded columellar margin, and obliquely narrow and ovate aperture, while *Curvella* possesses a straight columella, expanded columellar margin, and more vertical, higher, and broader oblong aperture.

Table 3. Comparison of terminal part of male genitalia between *Glessula* and *Rishetia*. References: 1 = Semper (1874); 2 = Godwin-Austen (1918); 3 = Godwin-Austen (1920); 4 = Schileyko and Kuznetsov (1996); 5 = Schileyko (1999); 6 = Budha et al. (2017). n/a = data not available (not mentioned in the description or could not differentiated from the original figure).

Species	Epiphallic caecum	Flagellum	References
***Glessula* von Martens, 1860**			
G. hebetata Godwin-Austen, 1920	absent	comb-like with numerous notches	6
G. inornata (Pfeiffer, 1853)	absent	comb-like with numerous notches	3
G. oakesi Godwin-Austen, 1918	absent	comb-like with three notches	2, 3
G. ochracea Godwin-Austen, 1918	absent	comb-like with numerous notches	2, 3
G. orobia (Benson, 1860)	absent	comb-like with five notches	3, 6
G. orophila (Reeve, 1849)	absent	comb-like with numerous notches	1
G. serena (Benson, 1860)	absent	comb-like with numerous notches	5
G. tamakoshi Budha & Backeljau, 2017	absent	comb-like with numerous notches	6
G. mandalayensis sp. nov.	absent	absent	This study
***Rishetia* Godwin-Austen, 1920**			
R. garoense (Godwin-Austen, 1920)	n/a	long cylindrical	3
R. hastula (Benson, 1860)	short knob-like	short tubular	6
R. kathmandica Budha & Backeljau, 2017	short cylindrical	long cylindrical	6
R. longispira (Godwin-Austen, 1920)	n/a	long cylindrical	3, 6
R. mastersi (Godwin-Austen, 1920)	short cylindrical	long cylindrical	6
R. nagarjunensis Budha & Naggs, 2017	short knob	short knob	6
R. rishikeshi Budha & Naggs, 2017	short cylindrical	long cylindrical	6
R. subulata Budha & Naggs, 2017	short cylindrical	long cylindrical	6
R. tribhuvana Budha, 2017	short cylindrical	long cylindrical	6
R. tenuispira (Benson, 1936)	short cylindrical	long cylindrical	4, 5

Glessula is widely distributed throughout the Indian subcontinent, and nearly 100 species have been described (Godwin-Austen 1920; Schileyko 1999; Ramakrishna et al. 2010; MolluscaBase 2023). Among the sporadic species recorded in Southeast Asia, Myanmar has 12 species (Gude 1914; Godwin-Austen 1920), while two species, *G. latestriata* von Möllendorff, 1899 and *G. paviei* Morlet 1893, have been recorded from Vietnam, Laos, and Thailand, and another two species, *G. sumatrana* (von Martens, 1864) and *G. wallacei* (Pfeiffer, 1856) from Indonesia (Tenison-Woods 1888; van Benthem Jutting 1952; Solem 1966; Schileyko 2011; Inkhavilay et al. 2019).

In this study, only five species including a new species, *G. blanfordiana* Nevill, 1877, *G. feddeni* Godwin-Austen, 1920, *G. gemma* (Reeve, 1850), *G. latestriata*, and *G. mandalayensis* sp. nov. have been collected and re-described.

8 *Glessula blanfordiana* Nevill, 1877

Fig. 5A–D, Table 1

Glessula blanfordiana Nevill, 1877: 26. Type locality: Ponsee, Yunnan [Ponsee, Kahkyen Hills, Yunnan Province, China]. Beddome 1906: 171. Pilsbry 1909: 98, pl. 13, fig. 11. Gude 1914: 437, 438. Godwin-Austen 1920: 56, pl. 164, fig. 21.
Stenogyra (*Glessula*) *blanfordiana*—Nevill 1881: 138, pl. 5, fig. 12.

Type specimens. ***Syntypes*** NHMUK 1988150 (2 shells; Fig. 5A, B) ex. Godwin-Austen collection from Ponsee, Yunnan, W. China.

Other material. Aik Kham Cave, Taunggyi Township, Taunggyi District, Shan State, Myanmar (20°49'07.0"N, 97°13'42.0"E): CUMZ 13067 (3 shells; Fig. 5C, D).

Description. Shell ovately conical, solid, brownish colour, and with 6–6½ whorls. Apex rounded; protoconch ~ 2 whorls with weak radial striations; subsequent whorls with equally and widely spaced ribs, more raised, and coarser near suture of last whorl. Spire regularly attenuated, slightly turreted; whorls convex; suture deep; last whorl largest. Aperture obliquely and narrowly ovate; peristome white and thickened; columella short, concave, slightly twisted and abruptly truncated. Umbilicus closed.

Distribution. This species was originally described from Yunnan, China, and subsequently reported from Bhamo, Kachin State, Myanmar (Nevill 1881). In this study, new material has been collected from Shan State, which borders Yunnan to the east and Bhamo to the north.

Remarks. When nominating this species, Nevill (1877: 26) compared it with *G. peguensis* (Blanford, 1865) from Bago and stated that *G. blanfordiana* has slender (less convex) whorls, wavy or curving, and stronger radial ribs. Nevertheless, the type specimens of these two species, *G. blanfordiana* (height 8–9 mm, Fig. 5A, B) and *G. peguensis* (height ~ 7 mm, Fig. 10B, C), exhibit considerable similarity in terms of shell shape and shell size. Therefore, more specimens from the Bago Region are necessary to ascertain whether the difference in shell sculptures represents variations or are taxonomically informative characters separating these two species.

Glessula blanfordiana examined herein are noticeably distinct from their congeners recorded in Shan State and Mandalay Region, namely *G. feddeni*

Godwin-Austen, 1920 and *G. latestriata* von Möllendorff, 1899. Specifically, *G. blanfordiana* has a shorter and bluntly attenuated spire, more bulging whorls, deeper suture, and stronger and densely radial ribbed sculptures. In contrast, the other species exhibit higher and pointed spires, more flattened whorls, and smooth to radial grooves sculptures (see Fig. 2D).

Glessula blanfordiana was described based on two specimens collected by J. Anderson during the Expedition to Yunnan and Upper Burma. The original description was very brief, without shell dimensions and illustrations. However, under the note of G. *ponsiensis* Godwin-Austen, 1920, states, 'The type from Ponsee, Yunnan (Plate CLXIV. fig. 20, apex) [= G. *blanfordiana*], has been sent me from Calcutta by the Director of the Zoological Survey of India, Dr. N. Annandale…' (Godwin-Austen 1920: 56). The NHMUK type collections contain a single lot with an original label stating 'Type' from 'Dr. J. Anderson', and collection locality from 'Ponsee'. These two specimens match well with the species description; both are figured herein for the first time. It is possible that N. Annandale may have gifted this type specimen lot to Godwin-Austen for comparison with other species, as was the case with other specimens from the Zoological Survey of India.

9 *Glessula crassilabris* (Benson, 1836)

Fig. 5E, F

Achatina crassilabris Benson, 1836: 353. Type locality: N.E. Frontier of Bengal. Pfeiffer 1848: 261. Reeve 1850: *Achatina*, pl. 21, fig. 81. Pfeiffer 1853: 493. Pfeiffer 1860: 313, pl. 25, figs 12, 13. Benson 1860: 464. Blanford 1865: 95.
Oleacina (*Electra*) *crassilabris*—Adams and Adams 1855: 105.
Achatina (*Electra*) *crassilabris*—Pfeiffer 1856: 168. Hanley and Theobald 1870: 17, pl. 36, fig. 1.
Cionella (*Glessula*) *crassilabris*—von Martens 1860: 254.
Stenogyra (Glessula) *crassilabris*—Nevill 1878: 170.
Glessula crassilabris—Godwin-Austen 1876: 315. Pfeiffer and Clessin 1881: 330. Beddome 1906: 169. Pilsbry 1909: 96, pl. 10, figs 14, 16. Gude 1914: 426. Godwin-Austen 1920: 39, 40, pl. 160, figs 14, 17–20, pl. 164, figs 16, 17. Ramakrishna et al. 2010: 157. Preece et al. 2022: 122, fig. 51e.

Type specimen. ***Syntype*** UMZC I.102430 (1 shell; Fig. 5E after Preece et al. 2022: fig. 51e) from Bengal.

Other material. NHMUK (1 shell; Fig. 5F) from Cherrapoonji (M10604/2). NHMUK 20200349 (2 shells) from N.E. Bengal. NHMUK 20200350 (2 shells) M.10695/2 from Khasi.

Diagnosis. Shell oblong ovate and regularly attenuated; spire high conical; apex rounded; subsequent whorls with weak and irregularly spaced radial ridges, slightly stronger near suture, and fine radial groves present. Suture impressed and whorls slightly convex. Aperture ovate; columella strong, concave, and truncated.

Distribution. This species is known from India and Rakhine State, Myanmar (Godwin-Austen 1920).

Remarks. The taxonomic history and clarification status of the type specimens have recently been published in Preece et al. (2022). Blanford (1865: 95) reported a small variety of *Glessula crassilabris* based on specimens from 'Arakan' [Rakhine State] and 'Shan hills near Ava' [Shan Hills near Innwa], and also suggested that the latter specimen lot were possibly distinct from *G. crassilabris* s. s., although they were closely related. The following year, Godwin-Austen (1920) introduced the Shan hills specimens as *G. feddeni* Godwin-Austen, 1920, but the small variety from 'Arakan' has never been made available.

10 *Glessula feddeni* Godwin-Austen, 1920

Fig. 6, Table 1

Glessula feddeni Godwin-Austen, 1920: 58, pl. 162, fig. 15. Type locality: Shan Hills [Shan State, Myanmar].
Glessula feddeni var.—Godwin-Austen 1920: 58, pl. 163, fig. 14.

Type specimens. ***Syntypes*** NHMUK 1906.2.2.261 [re-registered in error as 1985142] (5 shells; Fig. 6A, B) ex. Blanford ex. Godwin-Austen collection from the Shan Hills, E. of Ava.

Other material. NHMUK 1906.3.3.41 (1 shell; Fig. 6C) ex. Blanford ex. Fedden collection labelled as 'var.' from the Shan Hills. Limestone hills (Apache Cement Factory), Pyinyaung Village, Meiktila District, Mandalay Region, Myanmar (20°49'39.1"N, 96°23'35.1"E): CUMZ 13068 (8 shells; Fig. 6D–F).

Description. Shell globosely conical, solid, glossy, brownish colour, and with 6½–7 whorls. Apex slightly pointed; protoconch ~ 2 whorls with smooth surface; subsequent whorls with strong, oblique, and equally spaced radial grooves that more distinct near suture. Spire attenuated, turreted and pointed; whorls flatly convex; suture deep; last two whorls almost equal and largest. Aperture narrowly and obliquely ovate; parietal wall straight; peristome white and thickened; columella short, concave, slightly twisted, and truncated. Umbilicus closed.

Distribution. This species was originally described from 'Shan Hills', but the precise type locality was not provided. In this study, *G. feddeni* was located in the Mandalay Region adjacent to the Shan Hills.

Remarks. Godwin-Austen (1920) clearly states the catalogue number 'Type No. 261.06.2.2' (NHMUK 1906.2.2.261) from the Shan Hills. The original description included an illustration and two sets of measurements. The Godwin-Austen's type lot in the NHMUK consists of five shells with an original handwritten label stating 'Type'. The two specimens with the largest shell height closest to the given measurements are here illustrated together with another shell from the syntype lot.

Godwin-Austen (1920: 58, pl. 163, fig. 14) also recognised another variety as 'var.' and illustrated specimen lot 'No. 41.06.3.3' (NHMUK 1906.3.3.41). Nevertheless, this entity has never been properly made available. The specimen lot NHMUK 1906.3.3.41 (Fig. 6C) labelled as 'var.' is excluded from the type series of this nominal species (ICZN 1999: Art. 72.4.1). However, this specimen has a more slender shell than the type series (Fig. 6A, B) and is possibly more closely related to *G. latestriata*, which is also distributed in the Shan State.

11 *Glessula gemma* (Reeve, 1850)

Fig. 7A–D, Table 1

Achatina gemma Reeve, 1850: pl. 22, fig. 123 (Benson MSS). Type locality: Barrackpore, Bengal. Pfeiffer 1853: 496. Benson 1860: 464.

Oleacina (*Electra*) *gemma*—Adams and Adams 1855: 105.

Achatina (*Electra*) *gemma*—Pfeiffer 1856: 168. Hanley and Theobald 1870: 17, pl. 36, fig. 7.

Cionella (*Glessula*) *gemma*—von Martens 1860: 254.

Stenogyra (*Glessula*) *gemma*—Nevill 1878: 170.

Glessula gemma—Pfeiffer and Clessin 1881: 331. Beddome 1906: 169. Pilsbry 1909: 97, pl. 13, figs 1, 3. Gude 1914: 428. Godwin-Austen 1920: 22. Raheem et al. 2014: 124, figs 78b, 79c, d. Preece et al. 2022: 235, 236.

Type specimen. The type specimen could not be located in the UMZC nor in the NHMUK collections (Raheem et al. 2014; Preece et al. 2022).

Other material. NHMUK 1946.10.16.45–53 (9 shells; Fig. 7A, B) ex. Benson collection from Bengal. Montawa Cave, Taunggyi City, Taunggyi District, Shan State, Myanmar. (20°45'15.9"N, 97°1'3.4"E): CUMZ 13069 (5 shells; Fig. 7C, D).

Description. Shell elongate ovate, solid, purple-black or yellowish colour, and with 6½–7 whorls. Apex blunt; protoconch ~ 2 whorls with smooth surface; subsequent whorls with smooth and glossy to weakly radial ribs. Spire grows evenly, is high and obtuse; whorls flatly convex; suture wide and shallow; last two whorls almost equal and largest. Aperture obliquely ovate; peristome moderately thickened and white; columella short, concave, and truncated. Umbilicus closed.

Distribution. *Glessula gemma* was originally described from India and then its range extended to Bangladesh (Gude 1914; Godwin-Austen 1920; Raheem et al. 2014). In Myanmar, this species has been recorded from the Rakhine State and now in the Shan State.

Remarks. The historical specimens NHMUK 1946.10.16.45–53 ex. Benson collection from Bengal is illustrated herein as an example.

Our specimens match well with the authenticated Reeve specimen of this species, although it is far from the type locality and previously reported region in the Rakhine State, Myanmar. Among all the *Glessula* species from Myanmar, *G. gemma* is superficially similar to *G. latestriata* from Shan State. In comparison, *G. gemma* has smooth shell surfaces, less turreted spire, and a shallow suture, while *G. latestriata* possesses well-developed grooves, a turreted and more attenuated spire, and a deeper suture.

12 *Glessula inedita* Godwin-Austen, 1920

Fig. 7E, F

Glessula ineditus Godwin-Austen, 1920: 58, 59. Type locality: Shan Hills [Shan State, Myanmar].

Type specimens. ***Syntypes*** NHMUK 1906.5.5.88 [re-registered in error as 1985228] (3 shells; Fig. 7E, F) ex. W.T. Blanford collection from Shan Hills.

Diagnosis. Shell oblong turreted and regularly attenuated; spire high conical; apex rounded; subsequent whorls with very weak irregularly spaced radial ribs. Suture deep and whorls convex. Aperture widely ovate; columella concave and truncated.

Distribution. This species is known to occur only from the type locality.

Remarks. The original description did not include an illustration, and one set of shell measurements was given. Godwin-Austen (1920: 58) clearly states, 'Type No. 88.06.5.5' (NHMUK 1906.5.5.88) is from the Blanford collection. This syntype lot consists of three shells, and the original label states 'Type'. The largest specimen matches well with the given measurements, and another shell from the same syntype lot is illustrated herein for the first time. No new materials have been reported to date.

13 *Glessula latestriata* von Möllendorff, 1899

Fig. 8A–D, Table 1

Glessula latestriata von Möllendorff, 1899: 166. Type locality: Kalow, Shan State [Kalaw Township, Taunggyi District, Shan State, Myanmar]. Beddome 1906: 172. Pilsbry 1909: 100. Gude 1914: 443. Godwin-Austen 1920: 59. Solem 1966: 93, 94, pl. 2, fig. e. Zilch 1973: 110, pl. 5, fig. 26. Inkhavilay et al. 2019: 49, fig. 20c, d.

Type specimens. ***Lectotype*** SMF 145919/1 (Fig. 8A) designated in Zilch (1973: pl. 5, fig. 26) from Kalow, Shan States. ***Paralectotypes*** SMF 227513/2 (2 shells) and NHMUK 1926.2.3.19–20 (2 shells; Fig. 8B) from Kalow, Shan States.

Other material. Thale Cumon Temple, Kalaw City, Shan State, Myanmar (20°43'24.1"N, 96°35'38.9"E): CUMZ 13070 (3 shells; Fig. 8C). Ywangan Village, near Lin Way Monastery, Kalaw Township, Taunggyi District, Shan State, Myanmar (21°13'43.3"N, 96°33'19.2"E): CUMZ 13071 (1 shell; Fig. 8D).

Description. Shell ovate conic, solid, glossy, brownish colour, and with 6½–7 whorls. Apex blunt; protoconch ~ 2 whorls with smooth to shallow radial grooves; subsequent whorls with distinctly thickened and equally spaced grooves. Spire gradually attenuated, slightly turreted, and bluntly pointed; whorls convex; suture deep; last two whorls almost equal and largest. Aperture narrow and obliquely ovate; peristome white and thickened; columella short, concave, slightly twisted, and truncated. Umbilicus closed.

Distribution. This species is known from Shan State in Myanmar, northern Thailand, and Laos (Gude 1914; Solem 1966; Inkhavilay et al. 2019).

Remarks. von Möllendorff (1899) described this species based on specimens collected by B Strubell from Shan State, Myanmar. The original description did not include any illustrations, and only one set of measurements was given. The species description was not explicitly based on one specimen. Nevertheless, Zilch (1973: 110) later used the terms 'Holotypus SMF 145919' and 'Paratypen SMF 227513/2' for the von Möllendorff type series in the SMF collection. This is not a valid holotype designation, but we consider it an inadvertent lectotype designation (ICZN 1999: Arts. 73.1, 74.5, and Recommendation 73F). The other specimens labelled as 'Paratypen SMF 227513/2' and 'Co-types NHMUK 1926.2.3.19–20' are considered paralectotypes.

Although both *G. latestriata* and *G. feddeni* possess radial grooves striations, the former has a slender shell, gradually attenuated spire, and blunter apex; in contrast, *G. feddeni* has a larger and broader shell, turreted, intermediately attenuated spire and pointed apex with abruptly truncate columella.

14 *Glessula mandalayensis* Man & Panha, sp. nov.

https://zoobank.org/01347449-D63E-469B-826C-BEE5D0D56B8E

Figs 8E, F, 9, Tables 1, 3

Type specimens. ***Holotype*** CUMZ 13072 (height 14.6 mm, width 7.1 mm; Fig. 8E), ***paratypes*** CUMZ 13073 (29 shells; Fig. 8F), NHMUK 20230922 (2 shells) and SMF (2 shells).

Type locality. Limestone Hills (Apache Cement Factory), Pyinyaung Village, Meiktila District, Mandalay Region, Myanmar (20°49'39.1"N, 96°23'35.1"E).

Etymology. The specific name *mandalayensis* is the name of region, where the type specimens of this species were collected.

Diagnosis. Shell large, globosely ovate; spire broad, almost cylindrically attenuated, turreted; last whorl largest; shell surface glossy, smooth to shallow grooves; aperture ovately rounded and broad; peristome thin and white.

Description. Shell globosely ovate, solid, glossy, brown to bright ochraceous colour, and with 6–7 whorls. Apex blunt and large; protoconch ~ 2 whorls with smooth surface; subsequent whorls with smooth to fine radial striations or sometimes with shallow grooves. Spire broad, cylindrically attenuated, turreted; whorls flatly convex; suture deep; last whorl largest. Aperture ovately rounded and broad; peristome white and thin; columella short, concave, and truncated. Umbilicus closed.

Genitalia (n = 1). Atrium very short. Penis evenly broad, stout, and thick muscularly. Epiphallus short, stout, slightly curved triangular shape, thick muscularly, smooth surface, and ~ 1/4 of penis length; flagellum absent. Penial retractor muscle long, thickened and attaches laterally at junction of penis and epiphallus. Vas deferens long distinct tube connected between tip of epiphallus and free oviduct and held in position to penis and vagina with weak connective tissue (Fig. 9A).

Vagina muscularly and nearly as long as penis. Gametolytic duct short and enlarged at base; gametolytic sac small and elliptical in shape. Free oviduct short and stout, and spermoviduct enlarged.

***Radula*.** Each row contains ~ 70+ teeth with half-row formula: central-lateral-marginal teeth (1–(19–20)–(15–16+)). Central tooth relatively small, symmetrical tricuspid with pointed central cusp and very small lateral cusps. Lateral teeth bicuspid: endocone long, slender and with pointed tip; ectocone small, pointed tip and located at base of teeth. Latero-marginal teeth gradually reduced in size and asymmetrically bicuspid: endocone short with pointed tip; ectocone small triangle on shape and situated around middle of tooth height. Outermost teeth small and becoming tricuspid; mesocone short and blunt tip; endocone and ectocone very small and pointed tips (Fig. 9B).

Distribution. This new species is known only from the type locality.

Differential diagnosis. *Glessula mandalayensis* sp. nov. can be distinguished from other congeners in Myanmar by having the largest and most globosely ovate shell, obtuse and broad spire, wide aperture, and thinner peristome. In particular, this new species differs from a sympatric species, *G. feddeni*, by having a larger size (height 13.3–16.0 mm; Table 1), more rounded shell, obtuse and broader turreted spire, wider aperture, thinner peristome, and smoother shell surface. In comparison, *G. feddeni* is smaller in size (height 7.8–10.8 mm; Table 1), with a more solid, slender conical shell, pointed and narrow spire, smaller aperture, thicker peristome, and with distinct grooves on the shell surface. *Glessula mandalayensis* sp. nov. can also be separated from *G. latestriata* by its broader shell, wider spire, and blunt apex with smoother shell surface. Whereas *G. latestriata* has a slenderer shell, narrowly attenuated spire and pointed apex with distinct radial grooves striations. This new species also differs from *G. gemma* by having a larger and globosely ovate shell (height 13.3–16.0; Table 1), more turreted spire, convex whorls, vertically elongated aperture, and deeper suture. Whereas *G. gemma* possesses a smaller and slender shell (height 8.7–9.2; Table 1), spire high conical, flatly convex whorls, more rounded aperture, and shallow suture.

Additionally, this new species differs from *G. crassilabris* s. s. from India and its variety from Rakhine State, Myanmar, in having a smoother shell, obtuse, and lower and broader spire. While *G. crassilabris* s. s. (Fig. 5E, F) displays stronger striations and a narrowly pointed spire (Blanford 1865).

Remark. So far, the genitalia of eight *Glessula* species has. The terminal part of the male genitalia of *G. mandalayensis* sp. nov. (Fig. 9A) clearly differs from these eight species in having no flagellum, while a flagellum is well-developed with a comb-like shape in the others (Table 3). However, we examined only a single specimen; therefore, the extent of variability within the species remains unknown.

15 *Glessula orophila* (Reeve, 1849)

Fig. 10A

Achatina orophila Reeve, 1849a: *Achatina*, pl. 19, species 105. Type locality: Neilgherry Hills, India [Nilgiri Hills, India]; Colombo, Ceylon. Benson 1860: 465.

Oleacina (*Electra*) *orophila*—Adams and Adams 1855: 106.

Cionella (*Glessula*) *orophila*—von Martens 1860: 254.

Stenogyra (*Glessula*) *orophila*—Nevill 1881: 137, pl. 5, fig. 19.

Glessula orophila—Beddome 1906: 168. Pilsbry 1909: 79, pl. 10, fig. 10. Gude 1914: 423. Raheem et al. 2014: 128, fig. 83a.

Type specimen. The type specimen could not be located from the UMZC and the NHMUK collections (Raheem et al. 2014; Preece et al. 2022).

Other material. NHMUK (3 shells + 2 juveniles; Fig. 10A) ex. Blanford collection from Mahableshwar.

Diagnosis. Shell ovate conical and regularly attenuated; spire low conical; apex rounded; subsequent whorls with very weak irregularly spaced radial ridges, and fine radial groves present. Suture shallow and whorls flattened. Last whorl large and ovate; aperture ovate; columella concave and truncated.

Distribution. This species was first introduced from India and later reported from Sri Lanka and Pegu [Bago Region, Myanmar] (Gude 1914: 423).

Remarks. *Glessula orophila* is listed in the doubtful name by Raheem et al. (2014). No Myanmar material has been examined, and only the literature record is known.

16 *Glessula peguensis* (Blanford, 1865)
Fig. 10B, C

Achatina peguensis Blanford, 1865: 78. Type locality: Irawady valley, Pegu [Ayeyarwady valley, Bago Region, Myanmar]. Pfeiffer 1868: 228. Hanley and Theobald 1874: 41, pl. 102, fig. 6.

Glessula peguensis—Theobald and Stoliczka 1872: 334. Pfeiffer and Clessin 1881: 331. Beddome 1906: 171. Pilsbry 1909: 99, pl. 13, fig. 12. Gude 1914: 438. Godwin-Austen 1920: 55, 56, pl. 162, figs 20, 21.

Stenogyra (*Glessula*) *peguensis*—Nevill 1878: 171.

Type specimen. The type specimen could not be located in the NHMUK collection.

Other material. NHMUK 1909.3.15.8 (3 shells; Fig. 10B, C) ex. Blanford collection from Thyet-Myo. NHMUK 20230920 ex. H.B.F. collection (4 shells) from Thyet Myo. SMF 235657/2 (2 shells) from Pegu.

Diagnosis. Shell oblong ovate and regularly attenuated; spire high conical; apex rounded and blunt; subsequent whorls with prominent regularly spaced radial ribs. Suture deeply impressed and whorls convex. Aperture widely ovate; columella strong, concave, and truncated.

Distribution. *Glessula peguensis* is distributed in Bago Region, Magway Region, and Rakhine State in Myanmar, as well as in Chittagong, Bangladesh (Gude 1914; Godwin-Austen 1920).

Remarks. The specimen from 'Thyet-myo', which is present in the Blanford collection with the original label as 'authentic', is illustrated herein as an example of this species. According to Godwin-Austen (1920: 56), this species is commonly found in Pegu.

The original type locality of this species was from a broad geographical range, 'Pegu', and the museum label stated Thyet-Myo as the collection locality. The reference to 'Pegu' and 'Thyet-Myo' on the original label needs to be clarified as to whether they refer to the same area or if there is a specific location in 'Thyet-Myo, Pegu'. The current administration area now includes 'Thyet-Myo' [Thayet Myo] as a district of the Magway Region located in central Myanmar, formerly part of 'Pegu, Lower Burma' during the British colonial period. Furthermore, Godwin-Austen (1920: 56) stated that additional specimens from 'Arakan near Tongoop' (No. 262.06.2.2) tended to have a larger shell size than the type specimen.

17 *Glessula perlevis* Godwin-Austen, 1920
Fig. 10D, E

Glessula perlevis Godwin-Austen, 1920: 59. Type locality: Shan Hills [Shan State, Myanmar].

Type specimens. ***Syntypes*** NHMUK 1906.5.5.89 [re-registered in error as 1986023] (5 shells; Fig. 10D, E) ex. Godwin-Austen collection from Shan Hills, Burma.

Diagnosis. Shell oblong ovate and regularly attenuated; spire high conical; apex rounded and blunt; subsequent whorls nearly smooth with very weak growth lines, and somewhat strong irregularly spaced ridges near suture.

Suture impressed and whorls slightly convex. Aperture ovate; columella concave and truncated.

Distribution. This species is known only from the type locality in the Shan Hills near Mandalay. The type locality noted by Godwin-Austen seems ambiguous because it was described as ‘probably comes from the Shan State near Mandalay collected by Fedden’ (Godwin-Austen, 1920: 59).

Remarks. Godwin-Austen (1920) described this species based on five specimens in the Blanford collection. The species description included one set of shell measurements, the number of specimens examined and the W.T. Blanford catalogue number ‘Type No. 89.06.5.5’ (NHMUK 1906.5.5.89), and there was no illustration of the shell. The NHMUK collections contain a type specimen lot consisting of five shells (2 matures + 3 immatures) with an original label stating ‘Types’. The mature shells correspond well with the shell dimensions given in the original description and are illustrated herein for the first time.

18 *Glessula ponsiensis* Godwin-Austen, 1920

Figs 10F, 11A, B

Stenogyra (*Glessula*) *pyramis* var. *major* Nevill, 1878: 169 [nomen nudum]. Type locality: Ponsee.

Glessula ponsiensis—Godwin-Austen, 1920: 56, pl. 164, fig. 19. Type locality: Ponsee, Yunnan.

Type specimens. ***Syntypes*** NHMUK 1989042 (1 shell; Fig. 10F) and NHMUK 1989043 (3 shells; Fig. 11A), both specimen lots collected by J. Anderson from Ponsee.

Other material. NHMUK 1912.4.16.747 (2 shells; Fig. 11B) ex. Beddome collection from Ponsee, Yunnan.

Diagnosis. Shell oblong turreted and regularly attenuated; spire high conical; apex rounded and blunt; subsequent whorls nearly smooth with fine growth lines, and strong, equally spaced radial ridges near suture. Suture impressed and whorls slightly convex. Aperture ovate; columella strong, concave, and truncated.

Distribution. *Glessula ponsiensis* was first described from Ponsee, Yunnan, and later discovered in Bhamao, Kachin State, situated on the upper part of Ayeyarwady River.

Remarks. The original description included a set of shell measurements and an illustration of the apex. Godwin-Austen (1920: 56) clearly states that this species was described based on specimens from the Indian Museum collection (now Zoological Survey of India (ZSI), Kolkata) collected by J. Anderson from Ponsee, which was misidentified as ‘*Stenogyra* (*Glessula*) *pyramis* Bs., var. *major* Nevill, 1878’. The name ‘var. *major*’ by Nevill (1878: 169) is unavailable (ICZN 1999: Art. 12). Under the note of the species, Godwin-Austen states, ‘I am fortunate in getting the type-shells for examination’. It seemed that he received on loan the type specimen (or specimens that were examined by Nevill (1878: 169)). The NHMUK type collections contain a specimen lot with two registration numbers, M10905/2 and 10906/2, which are ex-Indian Museum collection numbers where the original label states ‘*Stenogyra* (*Glessula*) *pyramis* Benson,

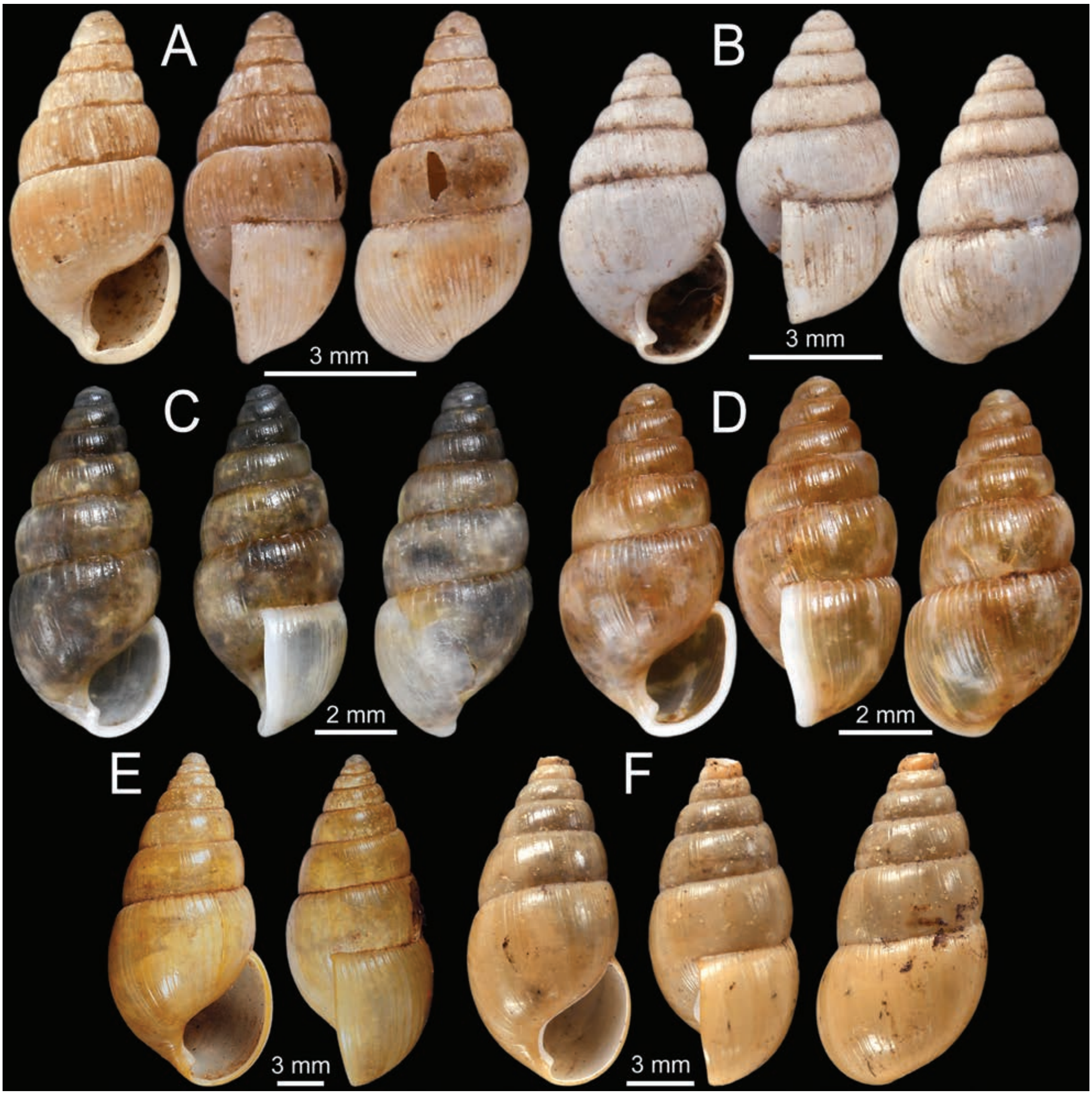


Figure 5. A–D *Glessula blanfordiana* **A, B** syntypes NHMUK 1988150 from Ponsee, Yunnan, W. China and **C, D** specimen CUMZ 13067 from Taunggyi, Shan State, Myanmar **E, F** *Glessula crassilabris* **E** syntype UMZC I.102430 from Bengal (after Preece et al. 2022: fig. 51e) and **F** specimen NHMUK from Cherrapoonji (M10604/2).

var. *major*', collection of 'Dr. J. Anderson' and with collection locality from 'Ponsee'. Interestingly, a species-group name was struck through and rewritten with red ink by Godwin-Austen, handwritten as '*ponsiensis*, G-A.' and with 'Type and three other one takes for B.M.'. It is probable that these specimens were presented to Godwin-Austen for examination. The specimen NHMUK 1989042 (1 shell has blue wool inside the shell; Fig. 10F) has a subsequent label stating 'holotype', and NHMUK 1989043 (3 shells; Fig. 11A) originates from the same Nevill type lot and has a subsequent label stating 'paratypes'. This is not a valid holotype designation (ICZN 1999: Arts 73.1, 73.2 and Recommendation 73F) and these specimens are considered as the syntypes, illustrated herein for the first time.

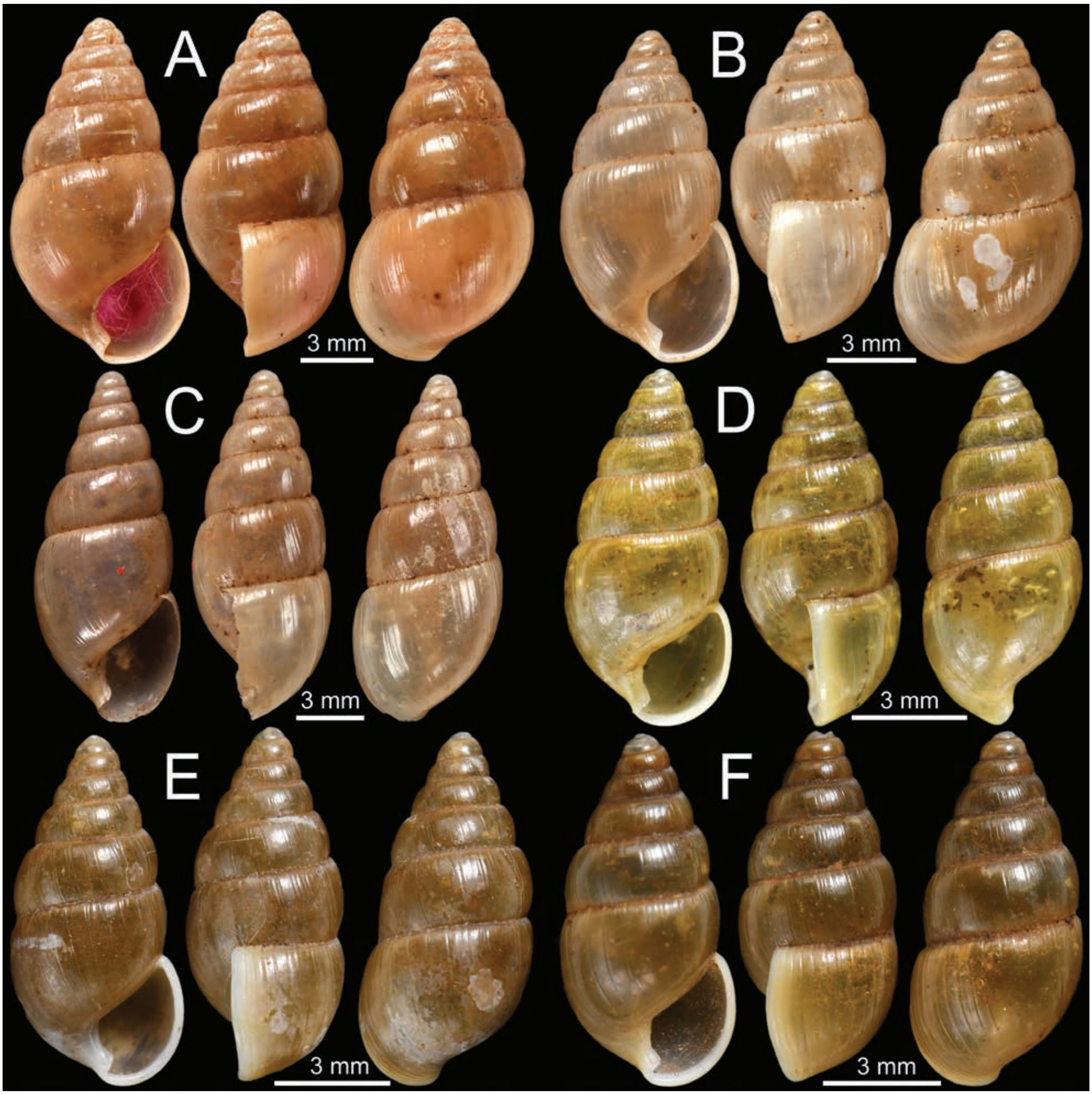


Figure 6. A–F *Glessula feddeni* **A, B** syntypes NHMUK 1906.2.2.261 from Shan Hills, E. of Ava **C** specimen NHMUK 1906.3.3.41 from Shan Hills and **D–F** specimen CUMZ 13068 from Pyinyaung Village, Mandalay Region, Myanmar.

19 *Glessula woodthorpei* Godwin-Austen, 1920

Fig. 11C–E

Glessula woodthorpei Godwin-Austen, 1920: 58, pl. 162, fig. 19. Type locality: Shan States [Shan State, Myanmar].

Type specimens. ***Syntypes*** NHMUK 1903.7.1.1628 [re-registered in error as 1986051] (9 shells; Fig. 11C–E) collected by Woodthorpe ex. Godwin-Austen collection from Shan States.

Other material. NHMUK 1903.7.1.3655 (2 shells) collected by Woodthorpe ex. Godwin-Austen collection from Siam N.W. Boundary.

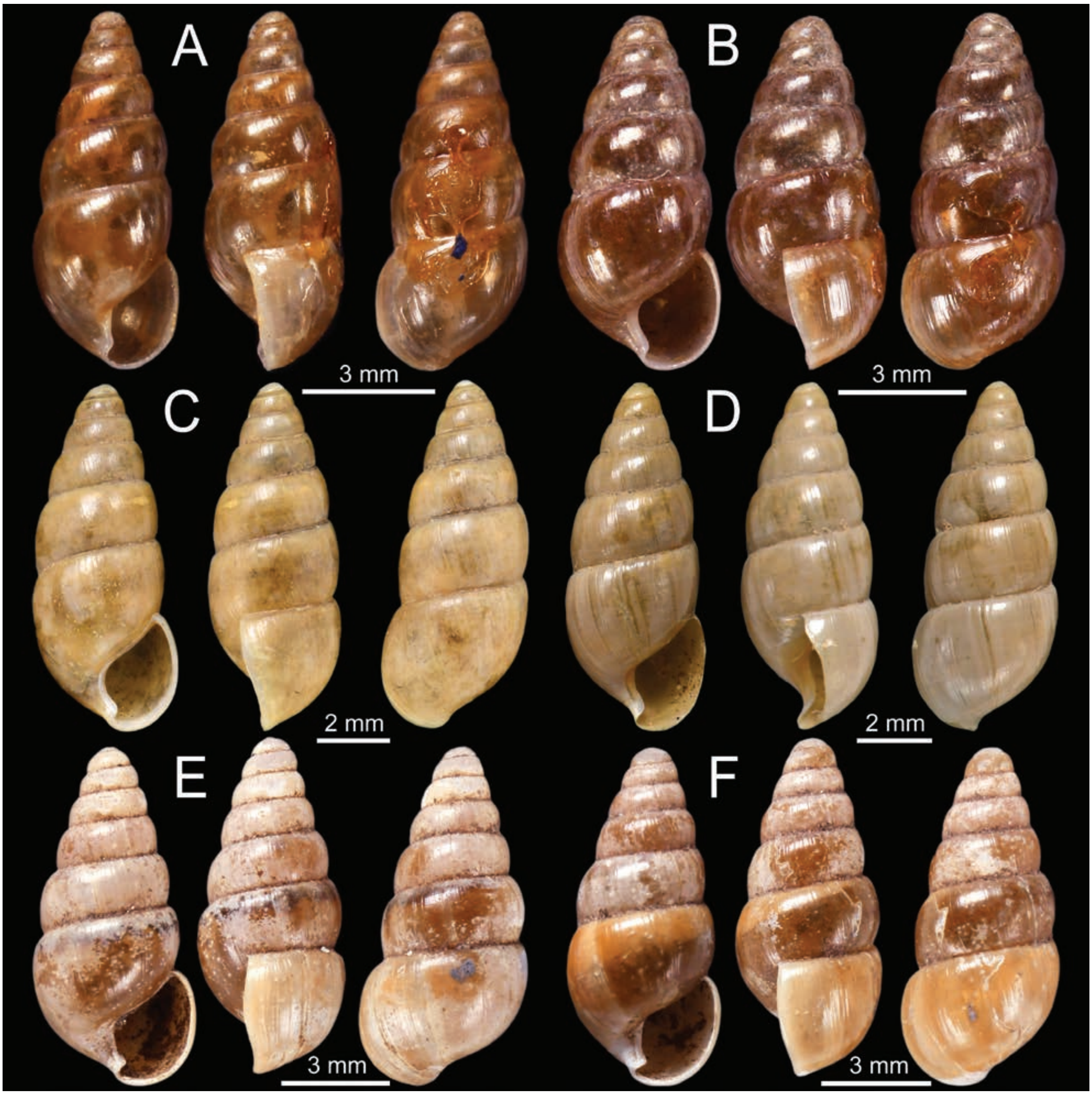


Figure 7. A–D *Glessula gemma* **A, B** specimen NHMUK 1946.10.16.45–53 from Bengal and **C, D** specimen CUMZ 13069 from Taunggyi, Shan State, Myanmar **E, F** *Glessula inedita*, syntypes NHMUK 1906.5.5.88 from Shan Hills.

Diagnosis. Shell oblong conical and regularly attenuated; spire high conical; embryonic whorls rounded; subsequent whorls nearly smooth and equally spaced radial ridges appeared near suture. Suture impressed and whorls slightly convex. Aperture ovate; columella strong, concave, and truncated.

Distribution. This species is known from Shan State, Myanmar with an additional record from Thailand.

Remarks. Godwin-Austen (1920) indicated that nine specimens with the catalogue number 'Type No. 1682 B.M.' were examined. The species description included one set of measurements and an illustration of one shell. The NHMUK type collections contain a lot of nine specimens from the

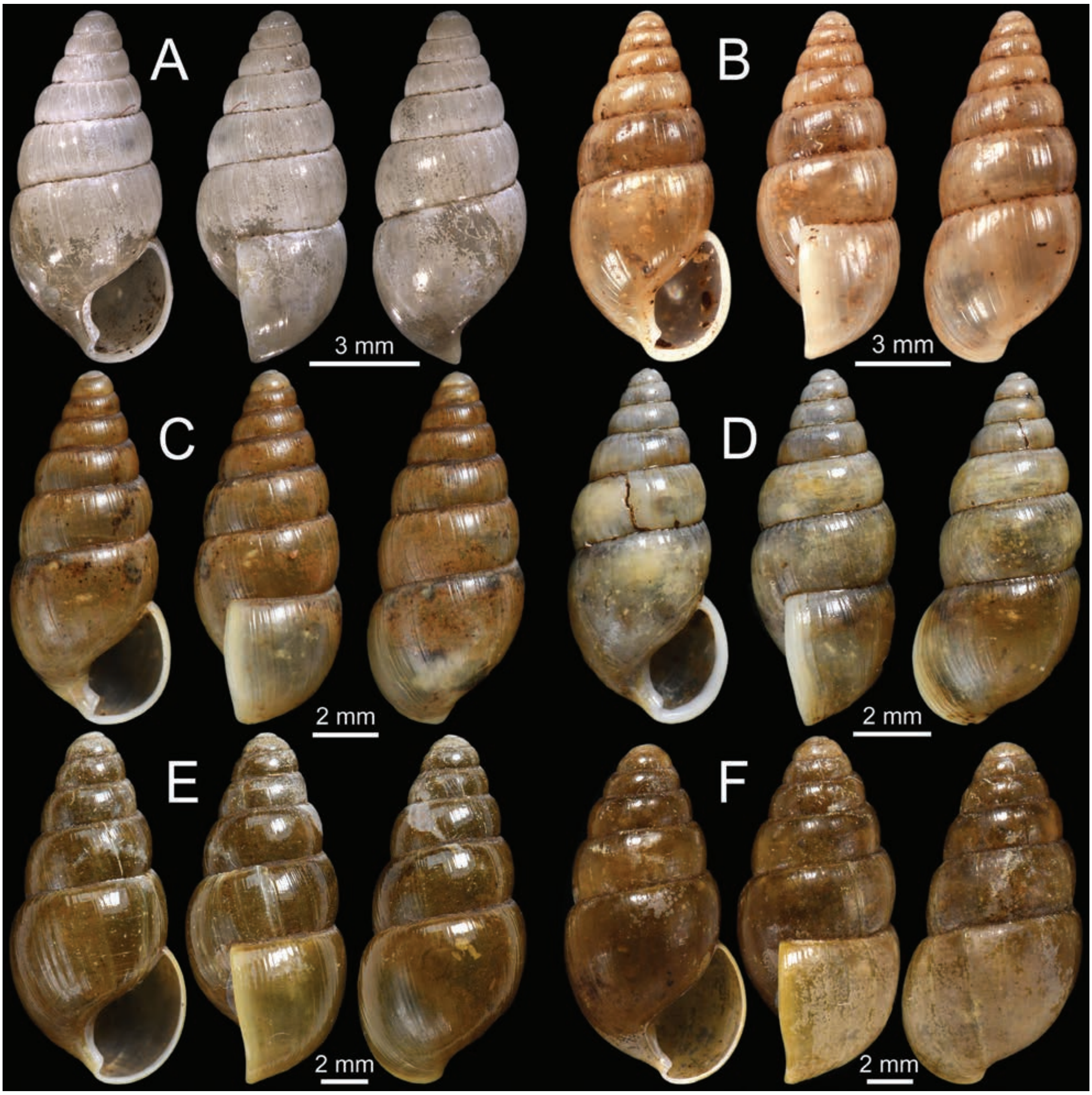


Figure 8. **A–D** *Glessula latestriata* **A** lectotype SMF 145919 from Kalow, Shan States **B** paralectotypes NHMUK 1926.2.3.19–20 from Kalow, Shan States **C** specimen CUMZ 13070 from Thale Cumon Temple, Kalaw, Shan State, Myanmar and **D** specimen CUMZ 13071 from Ywangan Village, Kalaw, Shan State, Myanmar **E, F** *Glessula mandalayensis* sp. nov. **E** holotype CUMZ 13072 from Pyinyaung Village, Mandalay Region, Myanmar and **F** paratypes CUMZ 13073 from the type locality. Photograph: Gojšina & Páll-Gergely (**A**).

Woodthorpe collection with a label in Godwin-Austen's handwriting stating 'Type'. The measurements of the specimen with red wool inside the shell are close to the measurements given in the original description. It likely corresponds to the illustration of the species provided in the original description and it herein figured (Fig. 11C) along with other shells (Fig. 11D, E) from the same syntype lot.

Godwin-Austen separately mentioned (1920: 58) another bleached specimen lot NHMUK 1903.7.1.3655 (2 shells) from Thailand. However, this specimen lot does not form part of the type series of this species.

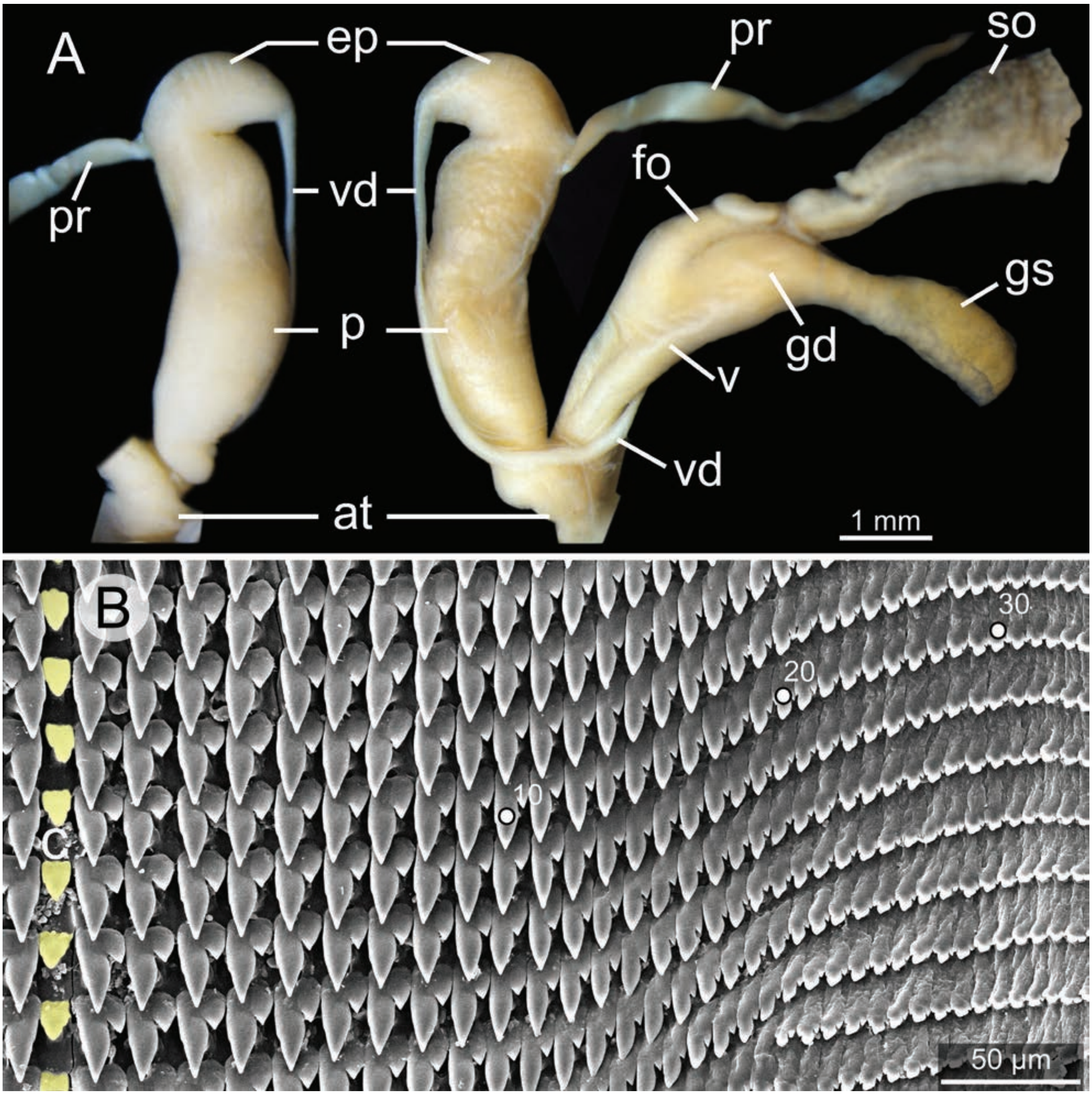


Figure 9. Genitalia and radula of *Glessula mandalayensis* sp. nov., paratype CUMZ 13073 from Pyinyaung Village, Mandalay Region, Myanmar **A** reproductive anatomy and **B** radula morphology: yellow colour and 'C' indicates central teeth row and numbers indicate tooth order from lateral to marginal end. Abbreviations: **at**, atrium; **ep**, epiphallus; **fo**, free oviduct; **gd**, gametolytic duct; **gs**, gametolytic sac; **p**, penis; **pr**, penial retractor muscle; **so**, spermoviduct; **v**, vagina; **vd**, vas deferens.

20 *Glessula yuangensis* Godwin-Austen, 1920

Fig. 11F

Glessula yuangensis Godwin-Austen, 1920: 59, pl. 162, fig. 18. Type locality: Yuang Ha, Siam Boundary [Mong Yawng Township, Tachileik District, Shan State, Myanmar].

Type specimen. ***Holotype*** NHMUK 1903.7.1.1312 [re-registered in error as 1986052] (Fig. 11F) collected by Woodthorpe ex. Godwin-Austen collection from Yuang Ha, Shan States.

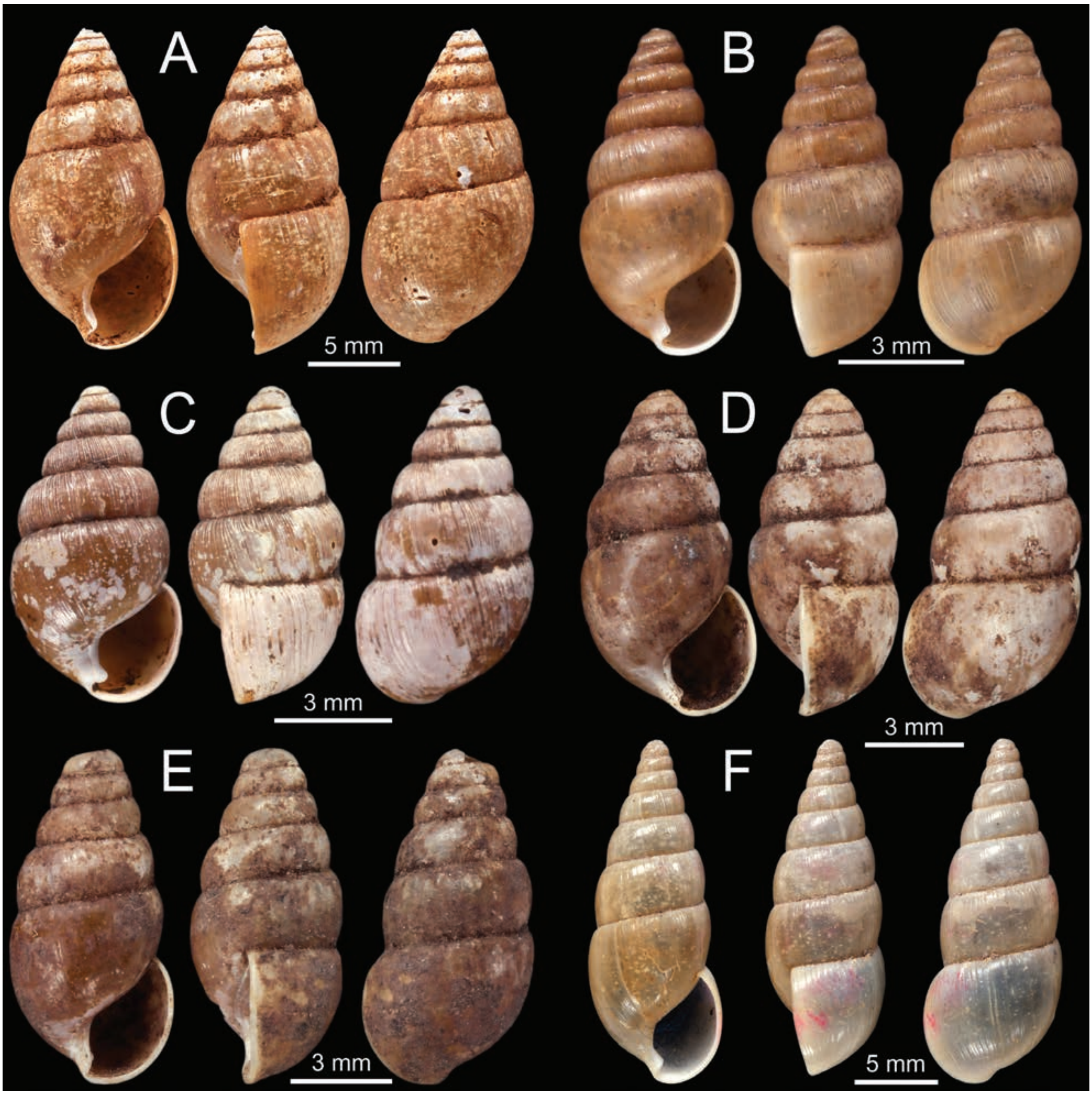


Figure 10. A *Glessula orophila*, specimen NHMUK ex. Blanford collection from Mahableshwar **B, C** *Glessula peguensis*, specimen NHMUK 1909.3.15.8 from Thyet-Myo **D, E** *Glessula perlevis*, syntypes NHMUK 1906.5.5.89 from Shan Hills, Burma **F** *Glessula ponsiensis*, syntypes NHMUK 1989042 from Ponsee.

Diagnosis. Shell oblong turreted and regularly attenuated; spire high conical; apex rounded and blunt; subsequent whorls with prominent wide spaced radial ribs, and radial groves present. Suture impressed and whorls slightly convex. Aperture ovate; columella strong, concave, and truncated.

Distribution. The species is currently known only from its type locality.

Remarks. Godwin-Austen clearly stated that this species was described based on only one specimen collected by R. Woodthorpe. The description included a set of shell dimensions and a shell illustration. There is one Godwin-Austen specimen lot, NHMUK 1903.7.1.1312, that has an original label stating ‘Type’ and is from

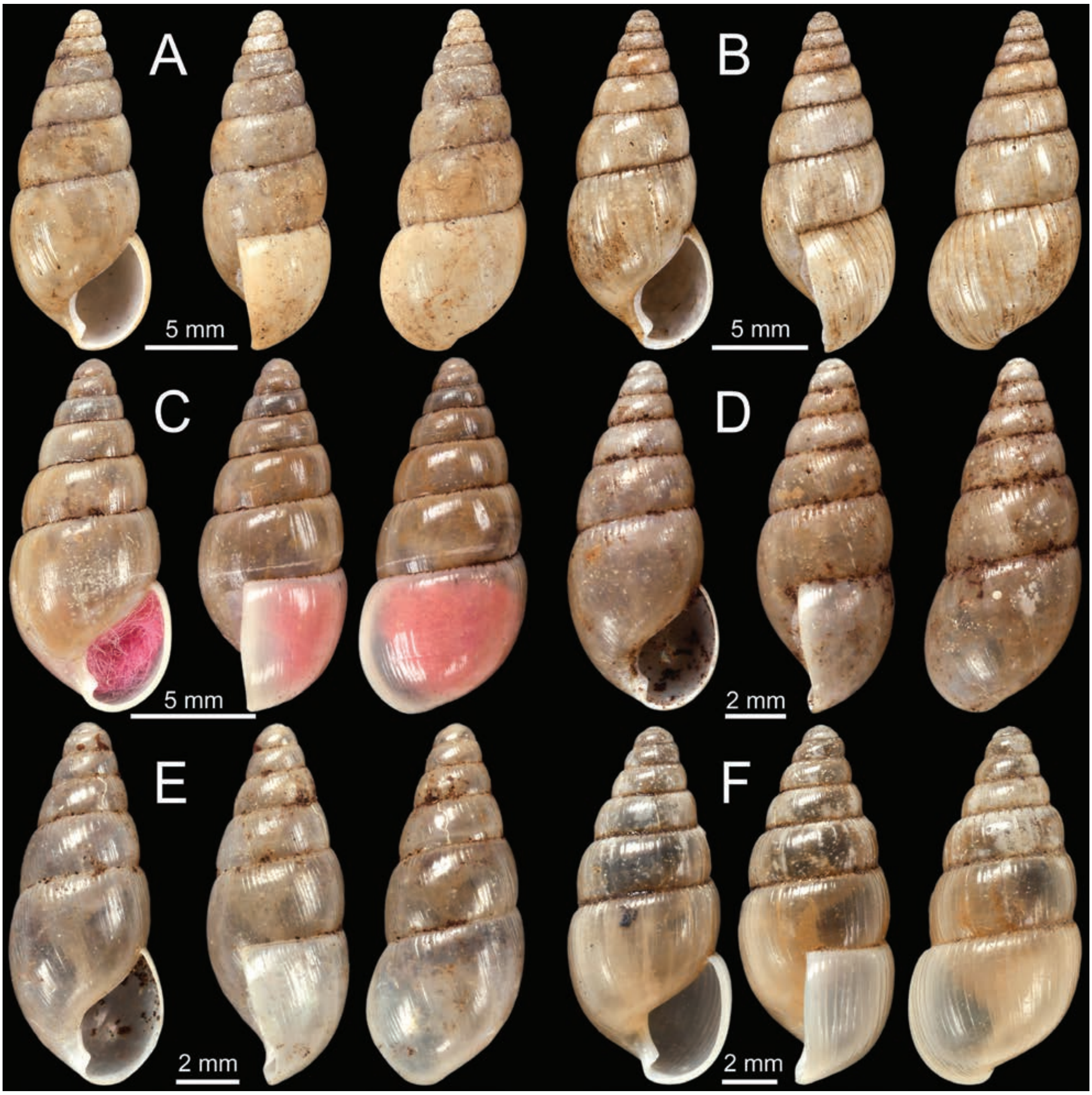


Figure 11. A, B *Glessula ponsiensis* **A** syntypes NHMUK 1989043 from Ponsee and **B** specimen NHMUK 1912.4.16.747 from Ponsee, Yunnan **C–E** *Glessula woodthorpei*, syntypes NHMUK 1903.7.1.1628 from Shan States **F** *Glessula yuangensis*, holotype NHMUK 1903.7.1.1312 from Yuang Ha, Shan States.

the Woodthorpe collection. We recognise this specimen as the holotype fixed by monotypy. Additionally, Godwin-Austen seemed to consider another specimen lot, ‘No. 1156 B.M.’ (NHMUK 1903.7.1.1156) from Kentung State [Kengtung Township, Shan State], as a distinct entity and it is therefore excluded from the type series.

Originally, the type locality was said to be from ‘Yuang Ha, Siam Boundary’; however, this town currently is found in the Shan State, Myanmar. The original type locality is now Mong Yawng Township, Shan State (~ 21°10'42.7"N, 100°21'24.3"E), Myanmar, with a further record from Kengtung, Shan State (Godwin-Austen 1920: 59).

Genus *Opeas* Albers, 1850

Bulimus (*Opeas*) Albers, 1850: 175, 176.
Stenogyra (*Opeas*)—von Martens 1860: 265, 266.
Opeas—Fischer and Crosse 1877: 592. Pilsbry 1906: 122. Gude 1914: 354. Zilch 1959: 351, 352. van Benthem Jutting 1952: 378. Schileyko 1999: 492.

Type species. *Helix goodallii* Miller, 1822 [junior homonym of Férussac (1821)] accepted as *Opeas hannense* (Rang, 1831), subsequent designation by von Martens in Albers (1860: 265).

Diagnosis. Shell small, slender, and conical; spire high, turreted, cylindrically, and gradually attenuated; embryonic whorls smooth; subsequent whorls with fine radial striations or growth lines. Aperture vertical, narrow, oblong, columellar margin expanded, and columella straight or concave. Umbilicus narrowly opened or closed. Penis cylindrical tube with short epiphallus, and flagellum and penial sheath absent; vagina long ~ 1/2 of penis length.

Remarks. *Opeas* and *Tortaxis* Pilsbry, 1906 generally resemble one another in having slender conical or cylindrical shells, nearly smooth to fine striations, and flatly convex whorls (Table 2). However, *Opeas* has a smaller size, straight columella, and mostly oblong aperture, whereas *Tortaxis* displays mostly larger size, nearly straight or slightly concave columella with a spiral fold, and more or less obliqued aperture. Likewise, *Opeas* is distinctly differentiated from *Bacillum* in that it is smaller in size, has a straight columella, fine shell sculptures and embryonic whorls which are narrowly rounded. In contrast, *Bacillum* exhibits a larger shell size, truncated and concave columella, stronger shell sculptures, and the embryonic whorls cylindrically rounded.

This genus is distributed in tropical and subtropical regions in Europe, Asia, Africa, and North America, and comprises nearly 200 species (Schileyko 1999; MolluscaBase 2023). In Myanmar, two species are recorded (Gude 1914).

21 *Opeas filiforme* von Möllendorff, 1894
Fig. 12A–C, Table 1

Opeas filiforme von Möllendorff, 1894: 151, pl. 16, fig. 11. Type locality: Golf von Siam: Samui-Inseln [Samui Island, Suratthani Province, Thailand]. Pilsbry 1906: 161, pl. 19, fig. 22. Zilch 1973: 120.
Prosopeas filiforme—Panha 1998: 32.

Type specimens. ***Lectotype*** SMF 227532 (Fig. 12A) von Möllendorff ex. C. Roebelen from Gulf von Siam: Samui-Inseln, designated in Zilch (1973: 120). ***Paralectotypes*** SMF 145657/7 (7 shells), SMF 227533/7 (7 shells).

Other material. Phra (Buddha) Cave, Tanintharyi Region, Myanmar (11°14'01.5"N, 99°10'42.8"E): CUMZ 13074 (15 shells; Fig. 12B, C).

Description. Shell slender and conical, translucent, whitish colour, and with 7½–8 whorls. Apex rounded; protoconch ~ 2 whorls, rounded and smooth surface; subsequent whorls generally nearly smooth with fine growth lines. Spire gradually and cylindrically tapering and largely turreted; whorls flatly convex and last whorl largest; suture deep and weakly crenulated. Aperture oblong; peristome thin; columella straight; columellar margin slightly expanded. Umbilicus narrowly opened to closed.

Distribution. This species occurs in peninsular Thailand and is newly recorded from the Tanintharyi Region, southern Myanmar.

Remarks. New discovered of this species were found in Tanintharyi, which borders the type locality of Thailand. The type specimen (Fig. 12A) possesses less turreted and more convex whorls than our specimens; however, this differentiation is herein considered an intraspecific variation. Compared to *O. innocens* Preston, 1910 from Mawlamyine, *O. filiforme* from Tanintharyi can generally be differentiated by its slender and more attenuated shell, slightly convex whorls, and turreted spire. However, a comprehensive examination of *O. innocens* specimens from the type locality is necessary to confirm this distinction.

22 *Opeas innocens* Preston, 1910

Opeas innocens Preston, 1910: 33, 34, fig. 2. Type locality: Khayon Cave, near Moulmein, Lower Burma [Khayon or Farm Cave, Mawlamyine Township, Mon State, Myanmar]. Gude 1914: 358.

Distribution. This species is known only from the type locality.

Remarks. No new specimens were found during our sampling conducted in Mawlamyine, Mon State. Furthermore, the authenticated and type specimens could not be located in the NHMUK collection, and currently, this species is known solely from the original description.

Genus *Paropeas* Pilsbry, 1906

Prosopeas (*Paropeas*) Pilsbry, 1906: 14. Zilch 1959: 353.
Paropeas—Naggs 1994: 175–191. Schileyko 1999: 508.

Type species. *Bulimus acutissimus* Mousson, 1857 by original designation.

Diagnosis. Shell slender and conical; spire high, turreted, and gradually attenuated; embryonic and subsequent whorls with irregularly dense, fine, or coarse radial striations. Aperture oblique, narrow or broadly ovate; columella concave; columellar margin expanded or not expanded. Penial simple, relatively long, slender, epiphallus short, flagellum absent, and penial sheath present; vagina ~ 1/2 of penis length and wider than penis.

Remarks. *Paropeas* can be distinguished from *Bacillum* and *Rishetia* by its irregularly coarse radial striations throughout the shell, less concave or straighter columella, and narrowly tapering and pointed embryonic whorls (Table 2). While *Bacillum* has stronger and more evenly spaced radial striations, deeper concave and truncate columella, and cylindrically tapering and obtuse embryonic whorls. Likewise, *Rishetia* has a glossy and smoother shell, broader whorls, more concave columella, and rounded and wider aperture (Pilsbry

1906; Gude 1914; Naggs 1994). In terms of genitalia, *Rishetia* is obviously distinct from *Paropeas* by having a tubular-shaped flagellum, while *Paropeas* has no flagellum (Naggs 1994; Schileyko 1999).

Paropeas and *Prosopeas* are very similar in terms of shell form and sculpture, but *Paropeas* possess stronger and more compact striations on embryonic whorls (Gude 1914; Naggs 1994). However, distinguishing between these two genera is still challenging, and precise identification requires further evidence, such as data on genitalia and molecular phylogeny.

This genus is mainly distributed in Southeast Asia. Seven recognised species are present, four are reported in Myanmar (Gude 1914; Naggs 1994; Schileyko 1999; MolluscaBase 2023).

23 *Paropeas swettenhami* (de Morgan, 1885)

Fig. 12D

Stenogyra swettenhami de Morgan, 1885: 389, pl. 6, fig. 6. Type locality: G. Tchöra, près d'Ipoh (Kinta) [Gunung Cheroh, Ipoh, Perak State, Malaysia].
Prosopeas swettenhami—Pilsbry 1906: 32, pl. 4, figs 11, 12. Laidlaw 1933: 216.
Paropeas swettenhami—Naggs 1994: 188.

Type specimen. ***Syntype*** MNHN-IM-2000-38930 (1 shell; Fig. 12D) from Malacca, G. Tchéhèl.

Diagnosis. Shell slender, elongate turreted and rapidly attenuated; apex pointed; subsequent whorls coarse with dense and fine radial striae. Suture wide and shallow, and whorls flattened. Aperture elongate ovate; columella concave.

Distribution. This species has been reported from Malaysia and Shan State, Myanmar (Naggs 1994).

Remarks. de Morgan (1885) describes *P. swettenhami* and *P. tchehelense* consecutively in the same publication and from a very close geographical area within Perak State, Peninsular Malaysia. Then von Möllendorff (1891: 337) suggests '*Stenogyra swettenhami* de Morgan, 1885' as a slight variation of *P. tchehelense*; therefore, some subsequent authors recognise the former as a synonym of the latter (i.e., Maassen 2001; MolluscaBase 2023). In contrast, Pilsbry (1906: 32) argues that they differ in shell shape and structure. We have examined the syntypes of both species and agree with Pilsbry (1906) that *P. swettenhami* (Fig. 12D) differs from *P. tchehelense* by having a slimmer shell, narrower aperture, cylindrical and rounded embryonic whorls. *Prosopeas tchehelense* (Fig. 12E) possesses a large, broad shell, wide aperture, convex, and rounded embryonic whorls.

No new materials of this species were found in this survey, and the type specimen is illustrated herein. Naggs (1994) provisionally reported the occurrence of *P. swettenhami* from Shan State, Myanmar. Considering the vast geographical distance between Perak and Shan State, it may be that the specimens Naggs (1994) regarded as *P. swettenhami* are, in fact, *P. terebralis* or another species. However, collecting topotypical material from Shan State, Myanmar, is necessary to confirm the existence of this species in Myanmar and the systematic relationship with *P. tchehelense*.

24 ***Paropeas terebralis*** **(Theobald, 1870)**

Fig. 12F

Stenogyra (*Opeas*) *terebralis* Theobald, 1870: 401. Type locality: Shan States [Shan State, Myanmar]. Nevill 1878: 166. Pfeiffer and Clessin 1881: 321.
Bulimus (*Stenogyra*) *terebralis*—Pfeiffer 1876: 133.
Prosopeas terebrale—Pilsbry 1906: 31. Gude 1914: 363.
Paraopeas terebralis—Naggs 1994: 188.

Type specimen. ***Syntype*** NHMUK 1888.12.4.1081 (1 shell; Fig. 12F) ex. Theobald collection from Shan States, Burma.

Diagnosis. Shell slender, elongate turreted and rapidly attenuated; apex obtuse; subsequent whorls coarse with dense growth lines throughout. Suture wide and shallow, and whorls slightly convex. Aperture elongate ovate and narrow; columella curved; peristome little acute.

Distribution. This species is only known from the type locality.

Remarks. No recent material of this species was collected in this survey, and the syntype is illustrated here for the first time. Gude (1914) recognised this species as belonging to the *Prosopeas*, but Naggs (1994) provisionally transferred this species to the *Paropeas* after comparing it with the type specimen.

Paropeas terebralis can be distinguished from *P. swettenhami* by its broader and more rounded embryonic whorls, deeper suture and slightly convex whorls, and coarse shell surface with dense growth lines. Whereas *P. swettenhami* possesses narrower and pointed embryonic whorls, shallower suture and flattened whorls, and shell surface with dense and fine radial striae.

25 ***Paropeas turricula*** **(von Martens, 1860)**

Fig. 12G, H, Table 1

Stenogyra turricula von Martens, 1860: 9. Type locality: Siam [Thailand]. von Martens 1867: 82, 83, pl. 22, fig. 7.
Paropeas turricula—Naggs 1994: 188. Maassen 2001: 81.
Prosopeas turricula—Pilsbry 1906: 30, 31, pl. 3, figs 95, 96. Inkhavilay et al. 2019: 52.

Type specimens. ***Syntypes*** NHMUK 1859.8.1.10 (3 shells; Fig. 12G) from Siam.

Other material. Phra (Buddha) Cave, Tanintharyi Region, Myanmar (11°14'01.5"N, 99°10'42.8"E): CUMZ 13075 (1 shell). The limestone karsts located close to Lampane Village, Tanintharyi Region, Myanmar (11°40'18.1"N, 99°13'30.1"E): CUMZ 13076 (2 shells; Fig. 12H).

Description. Shell slender, conical, translucent, whitish colour, and with 8–8½ whorls. Apex rounded; protoconch ~ 2 whorls, turreted and with nearly smooth to fine radial striations; subsequent whorls with dense and fine radial striations. Spire high, turreted, gradually, and cylindrically tapering; whorls flatly convex, last three whorls nearly equal; suture deep. Aperture narrowly ovate and elongate; peristome thin; columella truncated and concave; columellar margin slightly expanded. Umbilicus narrowly opened to closed.

Distribution. This species was first described in Thailand, then subsequently recorded in Laos and Malaysia (Naggs 1994; Maassen 2001; Inkhavilay et al. 2019), and is here reported from the Tanintharyi Region, Myanmar.

Remarks. *Paropeas turricula* can be differentiated from *P. tchehelense* by its slender shell, cylindrically turreted spire, and finer striations, while *P. tchehelense* has a broader and larger shell, a more rounded and broader spire, and stronger radial striations. This species can also be separated from *P. terebralis* from Shan State by having finer sculpture, flatly convex whorls, shallower suture, and embryonic whorls that are more turreted with nearly smooth to weaker striations, whereas *P. terebralis* displays a more elongated shell, thicker sculptures, more convex whorls, deeper suture, and embryonic whorls more rounded with stronger striations. *Paropeas swettenhami* has a larger shell, stronger striations, and wider and more deeply concave columella.

26 ***Paropeas walkeri*** (Benson, 1863)

Fig. 12I–L, Table 1

Spiraxis walkeri Benson, 1863: 90. Type locality: ad Portum Blair [Port Blair, Andaman Islands, India]. Pfeiffer 1868: 189. Hanley and Theobald 1873: 34, pl. 79, fig. 4.

Opeas walkeri—Theobald 1870: 395. Godwin-Austen 1895: 443. Blanford 1903: 280.

Stenogyra (*Opeas*) *walker*i—Nevill 1878: 165.

Stenogyra [*Spiraxis* (*Euspiraxis*)] *walkeri*—Pfeiffer and Clessin 1881: 323.

Prosopeas walkeri—Pilsbry 1906: 29, 30, pl. 6, fig. 70. Gude 1914: 363, 364. Ramakrishna et al. 2010: 183. Preece et al. 2022: 130, 131, fig. 56e.

Type specimens. *Syntypes* UMZC I.103115.A (5 shells; Fig. 12I, after Preece et al. 2022: fig. 56e) ex. R. McAndrew collection from Andaman Island.

Other material. NHMUK 1885.2.18.13–18 ex E.S. Berkeley collection Viper Id. Andamans: (6 shells; Fig. 12J). Aik Kham Cave, Taunggyi Township, Taunggyi District, Shan State, Myanmar (20°49'07.0"N, 97°13'42.0"E): CUMZ 13077 (3 shells; Fig. 12K). Ywangan Village, near Lin Way Monastery, Kalaw Township, Taunggyi District, Shan State, Myanmar (21°13'43.3"N, 96°33'19.2"E): CUMZ 13078 (2 shells; Fig. 12L).

Description. Shell slender, conical, translucent, whitish to pale yellowish colour, and with 8–8½ whorls. Apex rounded; protoconch ~ 2 whorls, rounded and with fine radial striations on entire whorls. Spire high, gradually tapering, and turreted; whorls flatly convex and last three whorls nearly equal; suture narrow and deep. Aperture narrowly ovate and elongate; peristome thin; columella straight or slightly concave; columellar margin simple to slightly expanded. Umbilicus narrowly opened to closed.

Distribution. This species was originally described from the Andaman Islands, India, and was later recorded in Shan State, Myanmar and Thailand (Gude 1914; Panha 1998).

Remarks. In Myanmar, *Paropeas terebralis* and *P. walkeri* are both recorded from Shan State. However, *P. walkeri* possesses broader, fewer, and more convex whorls, a straight columella with a slightly reflected columellar margin,

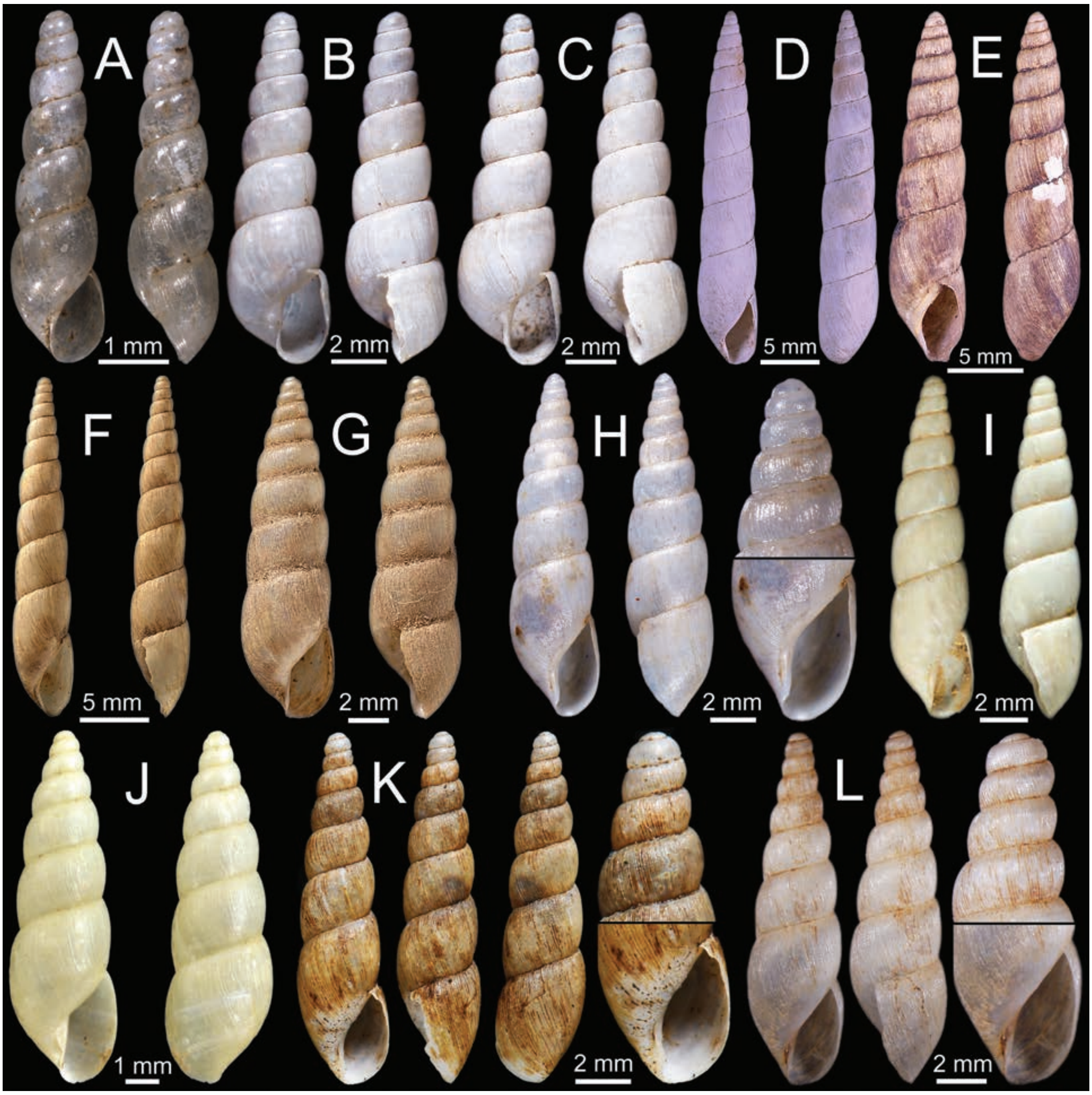


Figure 12. **A–C** *Opeas filiforme* **A** lectotype SMF 227532 from Gulf von Siam: Samui-Inseln **B, C** specimen CUMZ 13074 from Tanintharyi Region, Myanmar **D** *Paropeas swettenhami*, syntype MNHN-IM-2000-38930 from Malacca **E** *Paropeas tchehelense*, syntype MNHN-IM-2000-38932 from Pérak, Mont Tchéhèl **F** *Paropeas terebralis*, syntype NHMUK 1888.12.4.1081 from Shan States, Burma **G, H** *Paropeas turricula* **G** syntypes NHMUK 1859.8.1.10 from Siam and **H** specimen CUMZ 13076 from Tanintharyi Region, Myanmar **I–L** *Paropeas walkeri* **I** syntypes UMZC I.103115.A from Andaman Island (after Preece et al. 2022: fig. 56e) **J** specimen NHMUK 1885.2.18.13–18 from Viper Id. Andamans **K** specimen CUMZ 13077 from Taunggyi Township, Shan State, Myanmar with embryonic whorls and aperture and **L** specimen CUMZ 13078 from Kalaw Township, Shan State, Myanmar with embryonic whorls and aperture. Photographs: V Gojšina & B Páll-Gergely (**A**), P Bourguignon (**D, E**).

weaker radial striations, shallow suture, and embryonic whorls rounded. By contrast, *P. terebralis* has slimmer, higher, and flatter whorls, more concave columella, strong radial striations, deeper suture, and more pointed embryonic whorls. Additionally, *P. walkeri* also differs from *P. turricula* by its more convex whorls, straight columella, slightly reflected columellar margin, finer and crowded radial striations, deeper suture, and embryonic whorls rounded with stronger radial striations. Furthermore, *P. walkeri* can be differentiated from *P. swettenhami* by its slenderer shell, convex and closely grow whorls, deeper suture, more rounded protoconch whorls, distinctly turreted spire, and straight columella. *Prosopeas swettenhami* displays a broader shell, flatter whorls, shallow suture, convex protoconch whorls, less turreted spire, and more concave columella.

Among the specimens examined from Shan State, we observed shell variations, such as the columellar margin being either expanded or not expanded and the columella being straight or slightly concave. In addition, the specimen identified as *P. walkeri* from the Andaman Islands (Fig. 12J) exhibits a broader shell and a more expanded columellar margin compared to the syntype specimen (Fig. 12I).

Genus *Rishetia* Godwin-Austen, 1920

Glessula (*Rishetia*) Godwin-Austen, 1920: 7.
Rishetia—Schileyko 1999: 532. Raheem et al. 2014: 138, 139. Budha et al. 2017: 137. Preece et al. 2022: 127.

Type species. *Achatina tenuispira* Benson, 1836 by original designation.

Diagnosis. Shell slender and conical; spire high, turreted, and regularly attenuated; embryonic whorls smooth or with striations and subsequent whorls have thick or fine and equally or irregularly spaced radial ribs. Aperture oblique, narrow to broad, and ovate shape; columella concave and truncated; columellar margin not expanded. Penis large, thick, and moderately long; epiphallus relatively long; flagellum present with tubular shape; epiphallic caecum present; vagina enlarged, short ~ 1/2 of penis length.

Remarks. Originally, Godwin-Austen (1920) proposed *Rishetia* as a subgenus of *Glessula*, which Schileyko (1999) raised to the generic level, followed by Raheem et al. (2014), Budha et al. (2017), and Preece et al. (2022). *Rishetia* can be distinguished from *Glessula* by having a slender elongate-conical shell with a tubular-shaped flagellum and epiphallic caecum present, while *Glessula* processes an ovate-conical shell with a comb-like flagellum and epiphallic caecum absent (Tables 2, 3).

Rishetia can generally be differentiated from *Bacillum* by having a narrowly attenuated shell, convex and smaller apex, straight columella, and weak striations; *Bacillum* has a cylindrical shell, large and rounded apex, more concave columella, and stronger radial striations (Table 2). More information on the genitalia as well as a molecular phylogeny based on multiple species will clarify the systematic relationship of these two genera.

This genus has been documented in India, Sri Lanka, Bangladesh, and Nepal, with its presence in Southeast Asia limited to Myanmar (Godwin-Austen 1920; Schileyko 1999; Raheem et al. 2014; Budha et al. 2015, 2017). Currently, 23 species are recognised; among these, eleven species and subspecies have been documented from Myanmar (Godwin-Austen 1920; MolluscaBase 2023).

27 *Rishetia akouktoungensis* (Godwin-Austen, 1920), comb. nov.

Fig. 13A–C

Glessula akouktoungensis Godwin-Austen, 1920: 55. Type locality: Akouktoung on Irawady, Pegu [Akauk Taung (hill), Pyay District, Bago Region, Myanmar].

Type specimens. ***Syntypes*** NHMUK 1906.1.1.2207 [re-registered in error as 1985138] (6 shells; Fig. 13A–C). ex. W.T. Blanford ex. Godwin-Austen collection from Akouktoung, Pegu.

Diagnosis. Shell elongate, turreted, and regularly attenuated; apex rounded; subsequent whorls nearly smooth and with coarse radial ridges near suture. Suture impressed and whorls flattened convex. Aperture broadly ovate; columella strong, concave, and truncated.

Distribution. The species is currently known from its type locality, in which the modern name is Akauk Taung [hill, ~ 18°30'33.7"N, 95°06'48.5"E], south of Htone Bo (or Tonbo) Village, Padaung Township, Pyay District, Bago Region].

Remarks. The original description did not include an illustration, and only one set of measurements was given. Godwin-Austen's description was based on one lot of specimens which clearly stated 'Type No. 2207.06.1.1 B.M.' (NHMUK 1906.1.1.2207). There are six specimens from the NHMUK type collection with the original label stating 'Type'. The specimen that has a similar shell measurements as given in the original description and with pink wool inside the shell is figured herein (Fig. 13A). Other shells from the same syntype lot are also illustrated (Fig. 13B, C).

28 *Rishetia baculina* (Blanford, 1871), comb. nov.

Fig. 13D

Glessula baculina Blanford, 1871: 43, 44, pl. 2, fig. 6. Type locality: Khersiong Himalayae Sikkimensis. Beddome 1906: 160. Gude 1914: 379, 380. Godwin-Austen 1920: 14–16, pl. 159, fig. 7. Ramakrishna et al. 2010: 153.
Achatina (*Electra*) *baculina*—Hanley and Theobald 1873: 33, pl. 78, fig. 6.
Achatina baculina—Pfeiffer 1876: 291.
Stenogyra (*Glessula*) *baculin*a—Nevill 1878: 170.
Stenogyra (*Subulina*) *baculina*—Pfeiffer and Clessin 1881: 327.
Glessula tenuispira var. *baculina*—Pilsbry 1909: 88, 89, pl. 9, fig. 2.

Type specimens. ***Syntypes*** NHMUK 1909.3.15.9 [re-registered in error as 19850144] (3 shells; Fig. 13D) ex. Godwin-Austen ex. Blanford collection from Kursiong, Darjiling.

Diagnosis. Shell slender, elongate turreted and rapidly attenuated; apex rounded; subsequent whorls with fine and equally spaced radial ribs throughout. Suture impressed and whorls slightly convex. Aperture obliquely ovate; columella strong, concave, and truncated.

Distribution. This species was originally discovered in India and later reported from the Magway Region, Myanmar (Godwin-Austen 1920).

Remarks. Godwin-Austen (1920: 15) stated that specimens identified to this species in the Beddome collection were collected from 'Thyet Myo' [Thayet

District, Magway Region]. However, the Myanmar specimens show noticeable differences from the type specimens in having a more attenuated apex, and larger and broader aperture.

29 *Rishetia basseinensis* (Godwin-Austen, 1920), comb. nov.

Fig. 13E, F

Achatina pertenuis var. *major* Blanford, 1865: 79 [in part].
Glessula basseinensis—Godwin-Austen 1920: 54, pl. 161. fig. 3, pl. 164, fig. 12. Type locality: Bassein, Pegu and Pyema Khyoung, Bassein.

Type specimens. ***Syntypes*** NHMUK 1909.3.15.19 [re-registered in error as 1985139] (3 shells; Fig. 13E, F) ex. Blanford ex. Godwin-Austen collection from Bassein, Pegu.

Diagnosis. Shell slender, elongate turreted and regularly attenuated; apex rounded and blunt; subsequent whorls with fine and equally spaced radial ribs, which more prominent near suture. Suture impressed and whorls flattened convex. Aperture ovate; columella strong, concave, and truncated.

Distribution. *Rishetia basseinensis* appears to be restricted within Myanmar and is known only from the type locality. Based on the current administrative boundary, 'Bassien (or Pathein), Pegus' is in the Pathein Township, Pathein District, Ayeyarwady Region, rather than Pegu [Bago Region].

Remarks. Godwin-Austen (1920: 53) stated that when examining the type series of '*Glessula pertenuis* var. *major*' ex. Blanford collection, he found it very different from the nominotypical taxon, and described this specimen lot under a different name, '*Glessula basseinensis*'. In the original description, Godwin-Austen (1920: 54) provided two collection localities, namely 'Bassein, Pegu' and 'Pyema Khyoung, Bassein' and comparing three and six specimens, respectively. The description clearly states a catalogue number 'Type No. 19.9.3.15 B.M.' and includes an illustration of specimens from 'Bassein, Pegu'. The NHMUK collection contains this specimen lot NHMUK 1909.3.15.19 consisting of three shells with an original label in Godwin-Austen's handwriting stating 'Type' from the H.F. Blanford collection. The specimen with a similar shell measurement given in the original description and with pink wool inside the shell is figured herein (Fig. 13E). Additionally, one further shell from the same syntype lot is also illustrated (Fig. 13F).

The specimen lot NHMUK 1909.1.1.2208 is excluded from the type series of this species (see also under the *Rishetia pertenuis major*).

30 *Rishetia burrailensis maxwelli* (Godwin-Austen, 1920), comb. nov.

Figs 13G–I, 14A–C

Glessula (*Rishetia*) *burrailensis*, var. *maxwelli* Godwin-Austen, 1920: 45, 46, pl. 160, figs 5, 6. Type locality: Naga Hills, east of Kohima and Somra, Khulen Post. West of Kyendwin or Chindwin River, Upper Burma.
Glessula burrailensis, var. *maxwelli*—Godwin-Austen 1920: 61. Type locality: Somra Tracts, Somra Khulen Post, Upper Burma.

Type specimens. ***Holotype*** NHMUK 1903.7.1.1717/1 (Fig. 13G) ex. Godwin-Austen collection from Naga Hills, East of Kohima. ***Paratypes*** NHMUK 1903.7.1.1717/2–4 (3 shells; Fig. 13I) ex. Godwin-Austen collection from the location same as the holotype.

Other material. NHMUK 1903.7.1.3742 (7 shells + 1 broken shell; Fig. 14A, B) collected by F. Ede ex. Godwin-Austen collection from Somra Tracts, Somra Khulen Post, Burma (labelled as 'var. *somraensis*'). NHMUK 1903.7.1.3744 (2 shells; Fig. 14C) collected by F. Ede ex. Godwin-Austen collection from Somra Tracts, Somra Khulen Post, Burma (labelled as 'var. *somraensis*'). NHMUK 1988147 (4 shells; Fig. 13H) collected by L.R. Mawson from Somra Tracts, Somra Khulen Post, west of Kyengdwen River, Burma.

Diagnosis. Shell elongate, turreted, and regularly attenuated; apex rounded and blunt; subsequent whorls nearly smooth with fine irregularly spaced radial ridges throughout, and coarser ridges appearing near suture. Suture impressed and whorls flattened. Aperture ovate; columella concave and truncated.

Distribution. This subspecies was originally described from the Naga Hills. The locality reported in Myanmar is Somra Town (~ 25°21'43.6"N, 94°41'14.4"E), a mountainous area in Leshi or Layshi Township, Sagaing Region in northwestern Myanmar. It is neighbouring Nagaland to the west and Kachin State to the east and along the Chindwin River.

Remarks. The name *maxwelli* was stated twice in the same publication, on pages 45 and 61. The first mention is '*Glessula* (*Rishetia*) *burrailensis*, var. *maxwelli*'; when proposing this name, Godwin-Austen (1920: 45) recognised two specimen lots from Naga Hills… (collected by Col. H. St. P. Maxwell) and from Somra… Upper Burma (collected by F. Ede). Although the species description is brief, Godwin-Austen provides the catalogue number 'No. 1717 B.M.', two sets of shell dimensions, and illustrations of two shells from Naga Hill. We have examined this specimen lot, NHMUK 1903.7.1.1717, from Naga Hills, which consists of four shells. In the original description, Godwin-Austen (1920: 46) further states, 'Size: Fig. 5. Type' and in the figure caption as 'Fig. 5. (1st Type) from Naga Hills' and 'Fig. 6. (2nd Type) from Naga Hills'. It seemed that Godwin-Austen intended to designate the specimen figured in plate 160, fig. 5, as the unique name-bearing type, which we consider as the holotype. The other three specimens from the same lot are therefore paratypes.

The second mention is '*Glessula burrailensis*, var. *maxwelli*', for which Godwin-Austen (1920: 61) provided a very detailed description together with specimen lot number 'No. 3742 B.M.', two sets of shell measurements, from 'Somra Tracts, Somra Khulen Post, Upper Burma, but without illustration. The NHMUK collections contain specimen lot NHMUK 1903.7.1.3742, consisting of eight specimens with the original label stating 'var. *somraensis*, GA.'. This manuscript name has never properly been published and made available (ICZN 1999: Art. 10), the specimen lot NHMUK 1903.7.1.3742, with its original label stating 'var. *somraensis*' is considered as the syntype. Therefore, this second combination becomes an available name (ICZN 1999: Arts 11, 12), and it is considered a junior (primary) homonym (ICZN 1999: Arts 24.2.1, 24.2.2, 53.3, 57.2). Additionally, syntypes also include, NHMUK 1988147 (4 shells), from Somra, Khulen Post, West of Kyendwin River, Upper Burmah, as Godwin-Austen (1920: 61) recognised in the original description.

After examining the type specimens carefully, we found no differences in the diagnostic characters between the senior homonym (NHMUK 1903.7.1.1717/1 and NHMUK 1903.7.1.1717/2–4) and junior homonym (NHMUK 1903.7.1.3742, NHMUK 1903.7.1.3744 and NHMUK 1988147) specimens, especially shell shape, shell sculpture, and protoconch sculpture. The only detected difference is the brownish or yellowish brown periostracum, which we consider as intraspecific variation. Therefore, it seems unnecessary to propose a new replacement name for this junior homonym.

31 *Rishetia hastula* (Benson, 1860)

Fig. 14D

Achatina hastula Benson, 1860: 461. Type locality: ad Pankabari, prope Darjiling [Pankhabari, near Darjiling, West of Bengal, India]. Pfeiffer 1868: 235.

Achatina (*Electra*) *hastula*—Hanley and Theobald 1870: 9, pl. 18, fig. 4.

Stenogyra (*Glessula*) *hastula*—Nevill 1878: 169.

Stenogyra (*Subulina*) *hastula*—Pfeiffer and Clessin 1881: 327.

Glessula hastula—Theobald and Stoliczka 1872: 334. Beddome 1906: 167. Pilsbry 1909: 93, pl. 12, fig. 12. Gude 1914: 414. Ramakrishna et al. 2010: 161

Glessula (*Rishetia*) *hastul*a—Godwin-Austen 1920: 16, 17, pl. 161. figs 16, 17, pl. 163. figs 9, 9a, 10.

Rishetia hastula—Budha et al. 2017: 139, figs 2d, 6. Preece et al. 2022: 127, 128, fig. 55a.

Type specimen. ***Neotype*** NHMUK 1906.1.1.880 (designated in Preece et al. 2022: 127, fig. 55a) (Fig. 14D) ex. Blanford collection from Darjiling.

Diagnosis. Shell elongate, turreted, and regularly attenuated; apex rounded and blunt; subsequent whorls coarse with fine equally spaced radial ridges throughout. Suture somewhat impressed and whorls convex. Aperture broadly ovate; columella strong, concave, and truncated.

Distribution. The species was originally described from India and later recorded from Nepal (Ramakrishna et al. 2010; Budha et al. 2015; Kalita 2022). In Myanmar, it was reported from Kumah Hill and Maii [Ma-ei Town ~ 19°20'36.5"N, 94°08'21.9"E], which are in the Thandwe District, Rakhine State in the westernmost part of Myanmar (Theobald and Stoliczka 1872; Gude 1914; Godwin-Austen 1920).

Remarks. To clarify the taxonomic status of this species, Preece et al. (2022) have designated a neotype based on the specimen figured in Hanley and Theobald (1870, pl. 18, fig. 4). However, the image used to represent the neotype in Preece et al. (2022: fig. 55a) is an erroneous repetition of '*Achatina leptospira* Benson, 1865' (see Preece et al. 2022: fig. 51f). Therefore, the correct image of the neotype NHMUK 1906.1.1.880 is illustrated herein.

Theobald and Stoliczka (1872: 334) noted that the specimens from Arakan tended to differ from the type specimen in having a larger shell size. Nevertheless, Arakan and Sikkim are non-adjacent regions and far apart, which raises doubts about whether they are the same or distinct species.

32 *Rishetia kentungensis* (Godwin-Austen, 1920), comb. nov.

Fig. 14E, F

Glessula kentungensis Godwin-Austen, 1920: 57, 58. Type locality: Mong Sing, Siam Boundary [Muang Sing District, Luang Namtha Province, Laos]. Inkhavilay et al. 2019: 49, fig. 20b.

Type specimens. ***Syntypes*** NHMUK 1903.7.1.3650 [re-registered in error as 1986002] (3 shells + 1 juvenile; Fig. 14E, F) collected by Woodthorpe ex. Godwin-Austen collection from Mong Sing, Siam Boundary.

Other material. NHMUK 1903.7.1.3748 (4 shells) collected by Woodthorpe ex. Godwin-Austen collection from the Mekong River.

Diagnosis. Shell elongate, turreted, and regularly attenuated; apex rounded, blunt and with very large embryonic shell; subsequent whorls nearly smooth throughout, and prominent irregularly spaced radial ridges near suture. Suture impressed and whorls slightly flattened. Aperture broadly ovate; columella strong, concave, and truncated.

Distribution. This species was initially found in Laos; however, as noted by Godwin-Austen (1920), its presence in the Mekong River region is assumed to likely extend to the East Shan State.

Remarks. The original description gave the measurements for only one shell and did not include an illustration. Godwin-Austen (1920) clearly states the collection locality and the catalogue number ‘Type No. 3650 B.M.’. The NHMUK collections contain a lot of four specimens from the Godwin-Austen ex. Woodthorpe collection with an original label stating ‘Type’ and giving the collection locality as ‘Mong Sing, Siam Boundary’. The two specimens match well with the original description, and shell dimensions are illustrated herein. Another specimen, lot ‘No. 3748 B.M.’ from the ‘Mekong River’, is excluded from the type series of this nominal species.

Originally, the type locality was said to be from ‘Mong Sing, Siam Boundary’; currently, this locality refers to Muang Sing District, Luang Namtha Province, Laos. The specimen NHMUK 1903.7.1.3748, collected from the ‘Mekong River’ by Colonel R. G. Woodthorpe, has a vague locality that could possibly encompass the East Shan State (formerly Keng Tung State) and the Bokeo and Luang Namtha provinces in Laos.

33 *Rishetia limborgi* (Godwin-Austen, 1920), comb. nov.

Fig. 14G

Glessula limborgi Godwin-Austen, 1920: 56, 57. Type locality: Tenasserim [Tanintharyi Region, Myanmar].

Type specimen. ***Holotype*** NHMUK 1903.7.1.3200 [re-registered in error as 1985219] (Fig. 14G) collected by Limborg ex. Godwin-Austen collection from Tenasserim.

Diagnosis. Shell elongate, turreted and regularly attenuated; apex rounded; subsequent whorls with fine and equally spaced radial ridges throughout. Suture impressed and whorls flattened. Aperture broadly ovate; columella strong, concave, and truncated.

Distribution. This species is known only from the type locality and is likely endemic to that region.

Remarks. Godwin-Austen (1920) clearly states that this taxon was described based on only a single specimen collected by O. Limborg. The original description included only a single set of shell measurements but was without illustration. The NHMUK collections contain the type specimen lot, NHMUK 1903.7.1.3200 ex. Godwin-Austen ex. O. Limborg consisting of a single shell with an original label stating 'Type'. Therefore, we considered this shell as the holotype fixed by monotypy.

34 *Rishetia nathiana* (Godwin-Austen, 1920), comb. nov.

Fig. 14H, I

Glessula (*Rishetia*) *nathiana* Godwin-Austen, 1920: 54, 55. Type locality: Bassein District [Pathein District, Ayeyarwady Region, Myanmar].

Type specimens. ***Syntypes*** NHMUK 1906.1.1.2206 [re-registered in error as 1986018] (5 shells; Fig. 14H, I) ex. Blanford collection from Bassein District.

Diagnosis. Shell elongate turreted and regularly attenuated; apex rounded and blunt; subsequent whorls with very fine equally spaced radial ridges, which coarser near suture. Suture impressed and whorls flattened convex. Aperture broadly ovate; columella concave and truncated.

Distribution. *Rishetia nathiana* is known only from the type locality and is likely endemic to that region.

Remarks. Godwin-Austen clearly stated that the original description was based on a specimen lot, ex. W.T. Blanford collection with the catalogue number 'Type No. 2206.06.1.1 B.M.'. The NHMUK collections contain a lot of five specimens from the Godwin-Austen ex. Blanford collection with original label 'Type' and 'ex. duplicate collection'. The specimen matches well with the given shell measurements, and the original description is illustrated herein for the first time.

35 *Rishetia pertenuis pertenuis* (Blanford, 1865), comb. nov.

Fig. 15A–E

Achatina pertenuis Blanford, 1865: 79. Type locality: Tongoop, Arakan [Taungup Township, Rakhine State, Myanmar]. Pfeiffer 1868: 237.
Achatina (*Electra*) *pertenuis*—Hanley and Theobald 1870: 9, pl. 18, fig. 5.
Stenogyra (*Glessula*) *pertenuis*—Nevill 1878: 169.
Stenogyra (*Subulina*) *pertenuis*—Pfeiffer and Clessin 1881: 327.
Glessula pertenuis—Beddome 1906: 160. Gude 1914: 380. Godwin-Austen 1920: 52–54, pls 164, fig. 11, pl. 159, figs 1, 2. Ramakrishna et al. 2010: 170.
Glessula tenuispira var. *pertenuis*—Pilsbry 1909: 89, 90, pl. 9, fig. 3.

Type specimen. ***Possible syntypes*** NHMUK 1906.2.2.239 (7 shells; Fig. 15A, B) ex. Blanford collection from Henzada, Pegu and Tongoop, Arakan.

Other material. NHMUK 1888.12.4.1229–31 (3 shells; Fig. 15D, E) from Pegu. NHMUK 20230921 (5 shells) from Tongoop, Arakan (Fig. 15C).

Diagnosis. Shell slender, elongate turreted, and rapidly attenuated near apical whorls; apex rounded; subsequent whorls nearly smooth, fine growth lines, and with equally spaced ridges near suture. Suture impressed and whorls slightly convex. Aperture ovate; columella concave and truncated.

Distribution. This species was reported from several places in Myanmar: Henzada [Hinthada City, Ayeyarwady Region], Thayet Myo [Thayet City, Thayet District, Magway Region], Pegu [Bago Region], and Tongoop, Arakan [Taungup Township, Thandwe District, Rakhine State] (Nevill 1878; Gude 1914). It was also reported from Meghalaya State, India (Ramakrishna et al. 2010).

Remarks. The original description does not clearly state how many specimens were available to the author, although only one set of measurements was given. The NHMUK collection contains a lot of seven specimens from the Blanford collection with this species name. However, this is a mixed specimen lot of the same species as it consists of two collection localities, 'Henzada, Pegu' and 'Tongoop, Arakan', where only the latter was mentioned in the original description as the type locality. Therefore, this specimen lot NHMUK 1906.2.2.239 is considered as possible syntypes, from which two specimens are illustrated herein.

36 *Rishetia pertenuis major* (Blanford, 1865), comb. nov.

Fig. 15F, G

Achatina pertenuis var. *major* Blanford, 1865: 79. Type locality: Pyema Khyoung, Bassein District, Pegu [PyayMa Khaung or Pyinma Khuang, Pathein Township, Pathein District, Ayeyarwady Region, Myanmar].

Glessula pertenuis var. *major*—Gude 1914: 381. Godwin-Austen 1920: 53.

Type specimen. ***Possible syntypes*** NHMUK 1906.1.1.2208 (6 shells; Fig. 15F, G) ex. Blanford collection from Pyema Khyoung, Bassein; label state '*Glessula basseinensis* G-A.'

Diagnosis. Shell elongate, turreted and regularly attenuated; apex rounded and blunt; subsequent whorls with fine equally spaced radial ridges throughout, which coarser near suture. Suture impressed and whorls slightly flattened. Aperture broadly ovate; columella strong concave and truncated.

Distribution. This subspecies was known solely from the type locality.

Remarks. When describing '*Achatina pertenuis*', Blanford (1865) recognised the larger shells as a distinct variety and gave them the name 'var. *major*'. This taxon name was made available, although without description, because the two sets of shell dimensions and materials from 'Pyema Khyoung, Bassein district, Pegu' confer the indication (ICZN 1999: Arts 11.9 and 12).

The type series of the taxa could not be traced. Only one specimen lot from the Godwin-Austen collection belongs to W.T. Blanford's original type series., i.e., NHMUK 1906.1.1.2208, with the original label in Godwin-Austen's handwriting marked 'ex. duplicate collection Blf., intermediate between *A. tenuispira* and *A. pertenuis*', with a species name '*Glessula basseinensis* G-A.', and collection

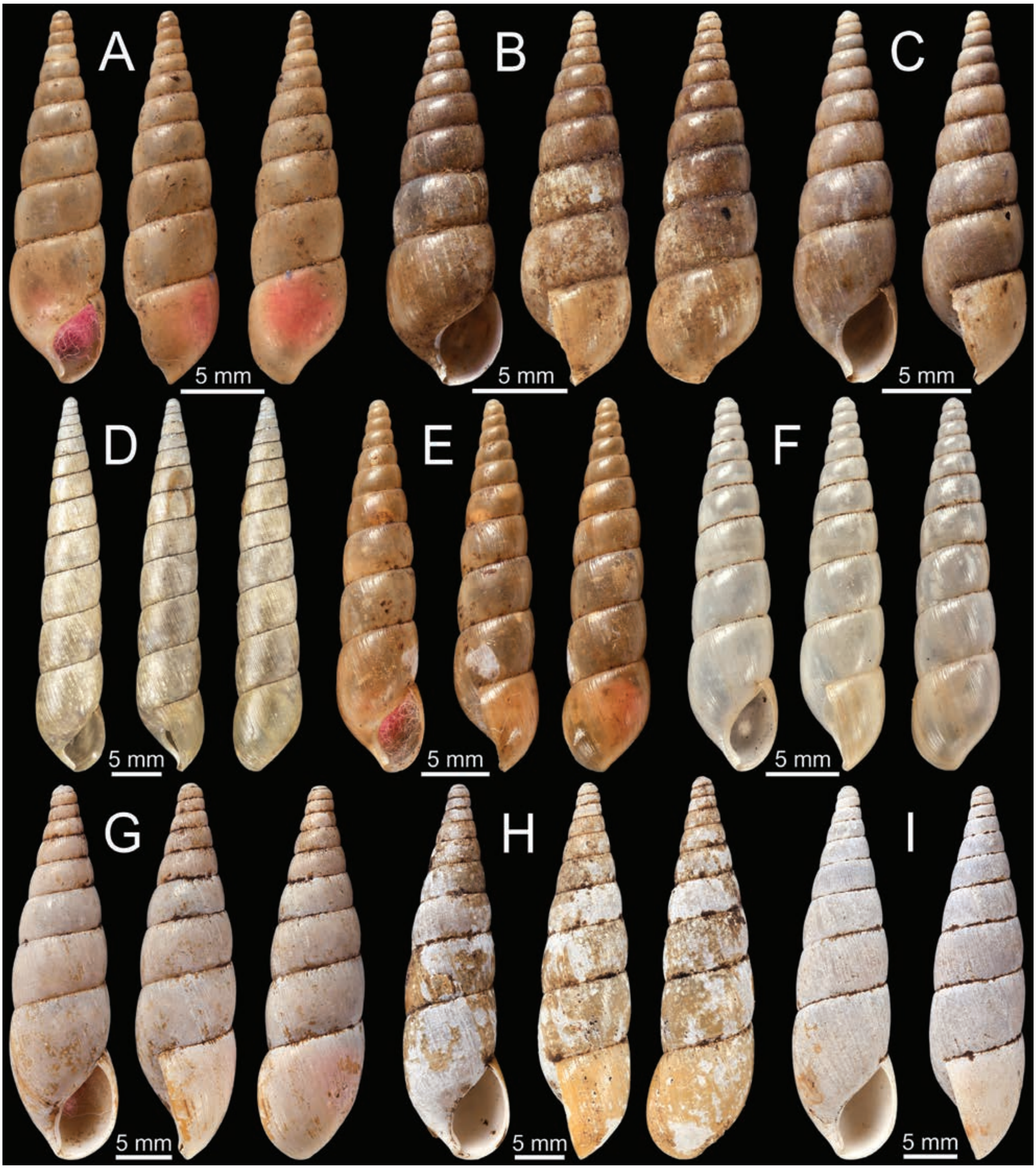


Figure 13. A–C *Rishetia akouktoungensis*, syntypes NHMUK 1906.1.1.2207 from Akouktoung, Pegu **D** *Rishetia baculina*, syntypes NHMUK 1909.3.15.9 from Kursiong, Darjiling **E, F** *Rishetia basseinensis*, syntypes NHMUK 1909.3.15.19 from Bassein **G–I** *Rishetia burrailensis maxwelli* **G** holotype NHMUK 1903.7.1.1717/1 from Naga Hills, East of Kohima **H** specimen NHMUK 1988147 from Somra Tracts, Somra Khulen Post, west of Kyengdwen River, Burma and **I** paratypes NHMUK 1903.7.1.1717/2–4 from Naga Hills, East of Kohima.

locality 'Pyema Khyoung, Bassein'. Therefore, this specimen lot is here considered as possible syntype material, and the two shells closest to the shell measurements given in the original description are illustrated herein.

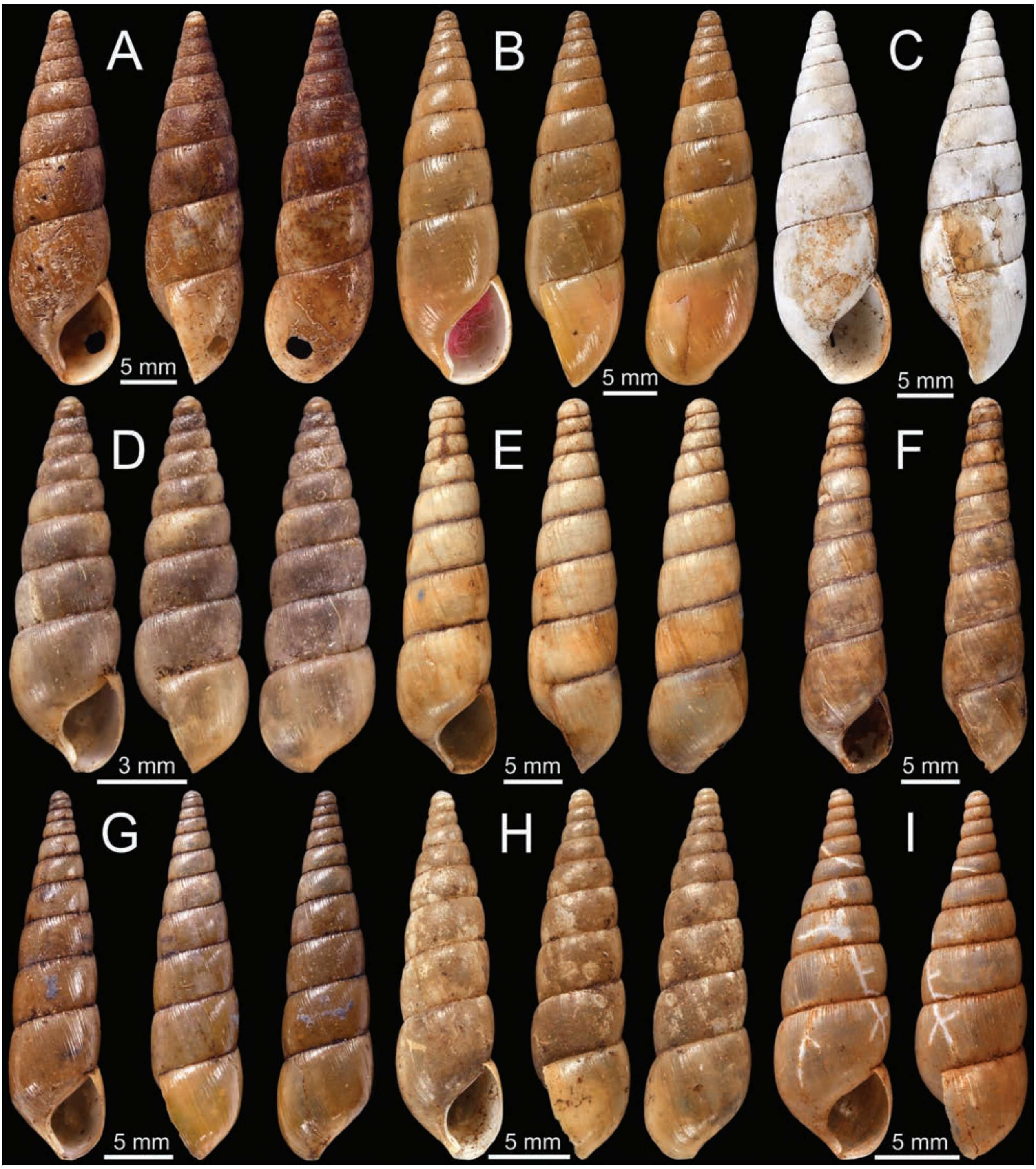


Figure 14. A–C *Rishetia burrailensis maxwelli* **A, B** specimen NHMUK 1903.7.1.3742 from Somra Tracts, Somra Khulen Post, Burma and **C** specimen NHMUK 1903.7.1.3744 from Somra Tracts, Somra Khulen Post, Burma **D** *Rishetia hastula*, neotype NHMUK 1906.1.1.880 from Darjiling **E, F** *Rishetia kentungensis*, syntypes NHMUK 1903.7.1.3650 from Mong Sing, Siam Boundary **G** *Rishetia limborgi*, holotype NHMUK 1903.7.1.3200 from Tenasserim **H, I** *Rishetia nathiana*, syntypes NHMUK 1906.1.1.2206 from Bassein District.

The modern name of 'Pyema Khyoung, Bassein District, Pegu' is the PyayMa Khaung or Pyinma Khuang (~ 18°38'51.7"N, 95°45'46.9"E), Pathein Township, Pathein District, Ayeyarwady Region, Myanmar.

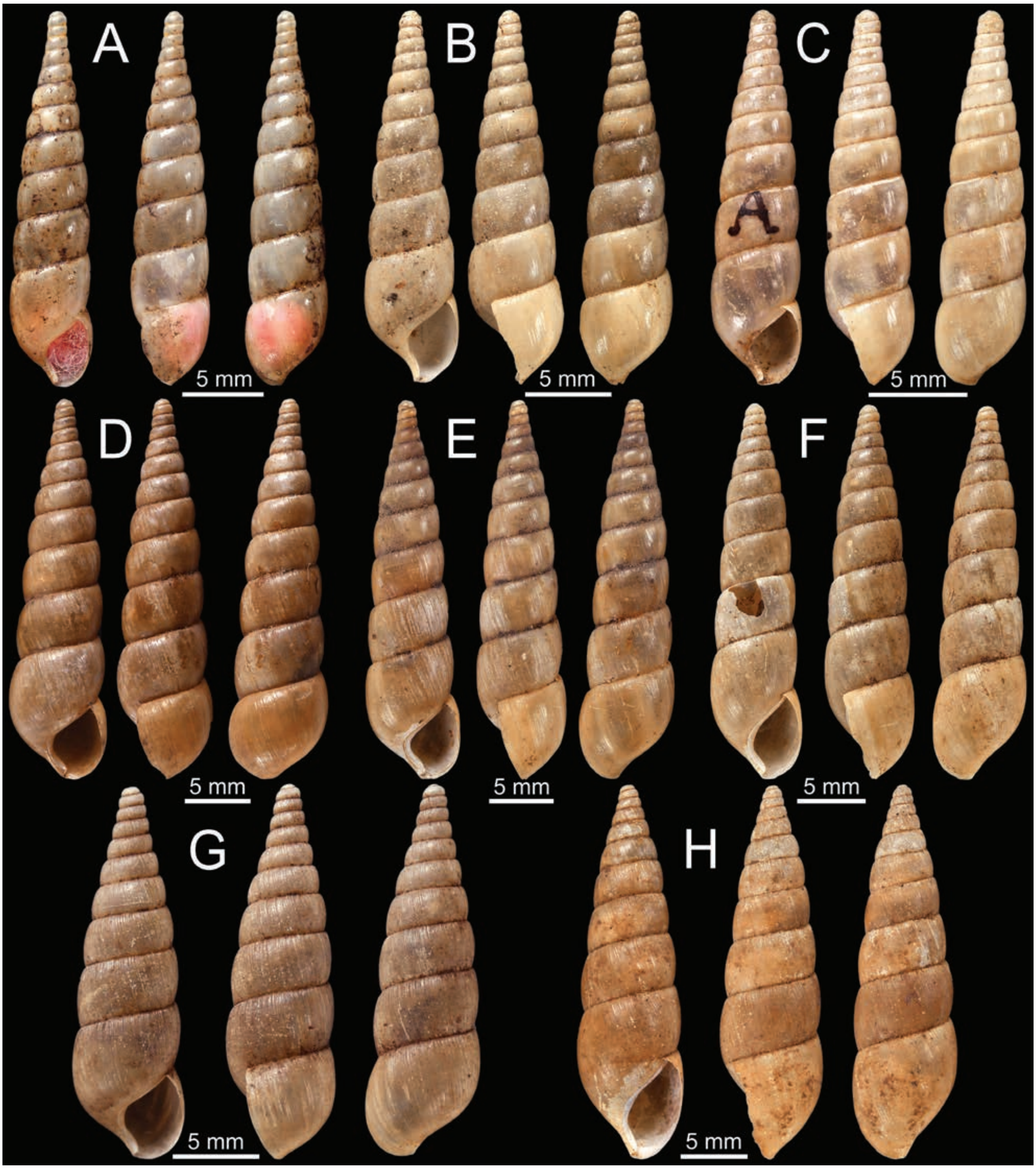


Figure 15. A–E *Rishetia pertenuis* **A, B** possible syntypes NHMUK 1906.2.2.239 from Henzada, Pegu and Tongoop, Arakan **C** specimen NHMUK from Tongoop, Arakan and **D, E** specimen NHMUK 1888.12.4.1229–31 from Pegu **F, G** *Rishetia pertenuis major*, possible syntypes NHMUK 1906.1.1.2208 from Pyema Khyoung, Bassein **H** *Rishetia tenuispira*, specimen NHMUK 1903.7.1.3332 from Garo Hills.

37 *Rishetia tenuispira* (Benson, 1836)
Fig. 15H

Achatina tenuispira Benson, 1836: 353. Type locality: N.E. Frontier of Bengal. Pfeiffer 1848: 262. Reeve 1849a: *Achatina*, pl. 16. Benson 1860: 464. Pfeiffer 1860: 310, 311 pl. 25, figs 6, 7. Blanford 1865: 95.

Subulina tenuispira—Adams and Adams 1855: 110.
Achatina (*Subulina*) *tenuispira*—Pfeiffer 1856: 169.
Achatina (*Electra*) *tenuispira*—Hanley and Theobald 1870: 17, pl. 36, fig. 8.
Stenogyra (*Glessula*) *tenuispira*—Nevill 1878: 169.
Stenogyra (*Subulina*) *tenuispira*—Pfeiffer and Clessin 1881: 327.
Glessula tenuispira—Beddome 1906: 160. Pilsbry 1909: 88, pl. 9, figs 1, 4. Gude 1914: 378. Godwin-Austen 1920: 31, 32.
Rishetia tenuispira—Raheem et al. 2014: 138, fig. 90c. Budha et al. 2017: fig. 14c. Preece et al. 2022: 128, fig. 55b.

Type specimen. The type specimen could not be located in the UMZC collection (Raheem et al. 2014; Preece et al. 2022). However, Budha et al. (2017: fig. 14a) figured a possible syntype of this species based on specimens ex. Benson collection from 'Teria Ghat', this specimen lot was not considered to form part of the type series by Preece et al. (2022).

Other material. NHMUK 1946.10.16.1–7 (7 shells) ex. R. McAndrew collection from Pegu. NHMUK 1903.7.1.3332 (1 shell; Fig. 15H) labelled as 'var.' ex. Godwin-Austen collection from Garo Hills. UMZC I.102045 from Teria Ghat (Budha et al. (2017: fig. 14a) recognised this specimen as a possible syntype).

Diagnosis. Shell elongate, turreted, and regularly attenuated; apex rounded; subsequent whorls with fine equally spaced radial ridges throughout and more prominent near suture. Suture impressed and whorls slightly flattened. Aperture elongate ovate; columella concave and truncated.

Distribution. This species is broadly distributed in Bangladesh, India, and Nepal (Budha et al. 2015; Preece et al. 2022). It was also reported from several localities in the southwest and eastern Myanmar: Ayeyarwady, Bago, and Tanintharyi regions (Benson 1860; Blanford 1865; Beddome 1906).

Remarks. Benson (1860: 464) reported that Theobald found a variety of '*Achatina tenuispira*' on the banks of Irrawaddy [Ayeyarwady River] and from Phie Than [probably in Tanintharyi Region]. Blanford (1865) recorded the presence of a small-sized species in Akoutoung [Akauk Taung, Ayeyarwady Region] and further south, while Beddome (1906) noted its occurrence in Pegu [Bago Region].

Genus *Tortaxis* Pilsbry, 1906

Tortaxis Pilsbry, 1906: 5, 6. Zilch. 1959: 347. Schileyko 1999: 534. Schileyko 2011: 10. Do and Do 2014: 455.

Type species. *Achatina erecta* Benson, 1842, by original designation.

Diagnosis. Shell slender, cylindrically shaped; spire high, mostly turreted, and gradually attenuated; embryonic whorls smooth, and subsequent whorls with nearly smooth to strong radial ribs. Aperture vertical, narrow, and oblong; columella concave or straight and with spiral fold below; columellar margin with or without expansion near umbilicus. Umbilicus narrowly opened or closed.

Remarks. *Tortaxis* can be distinguished from other subulinid taxa from Myanmar, namely *Allopeas*, *Opeas*, and *Bacillum*, by having a slender, cylindrical, and turreted spire, flatter whorls, smooth embryonic whorls, a large and rounded apex, and a distinct spiral fold on the columella (Table 2).

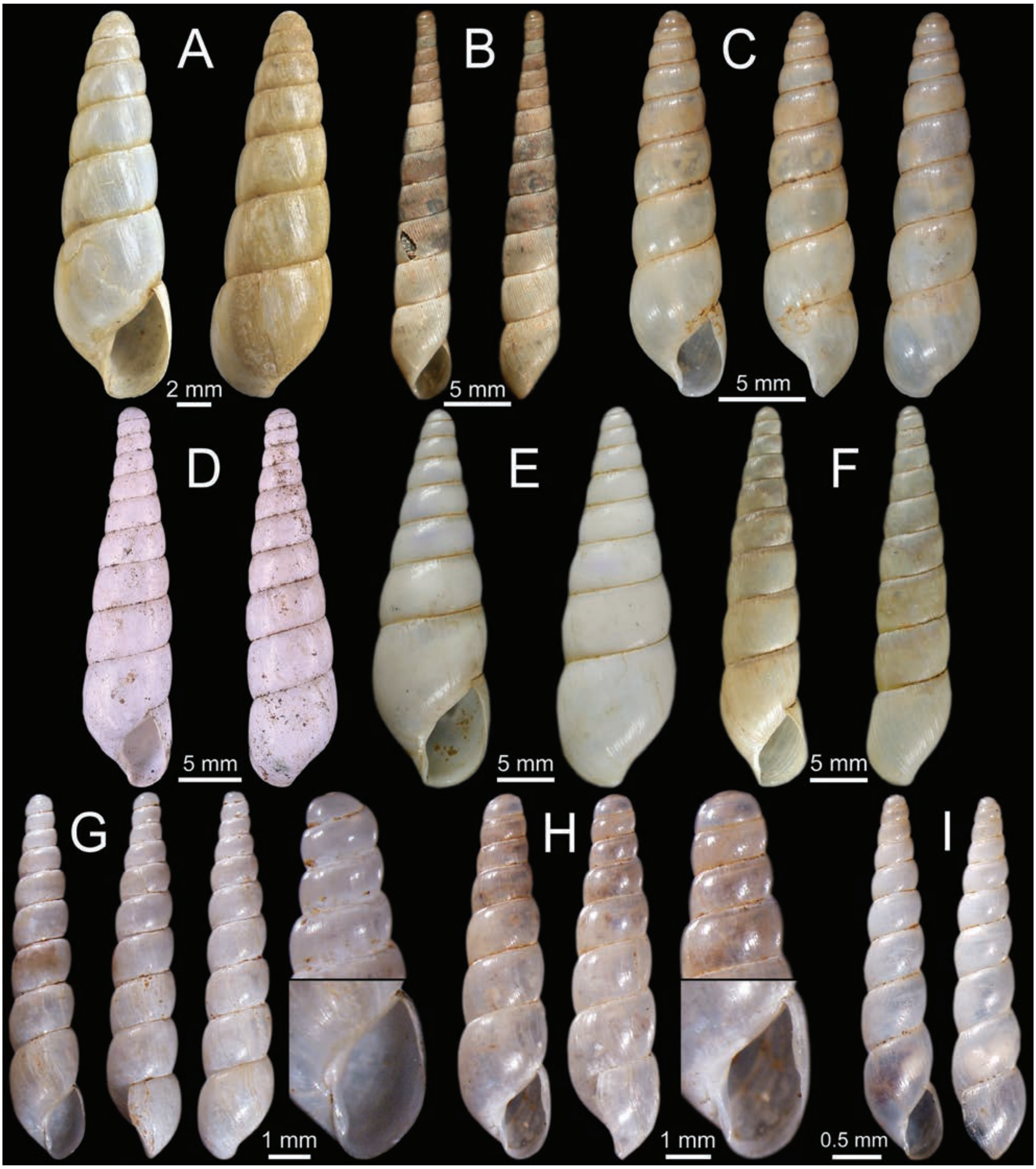


Figure 16. A *Tortaxis erectus*, neotype NHMUK 1991104A from Nanking, China **B** *Tortaxis elongatissimus*, syntype MNHN-IM-2000-4705 from Pac-Kha **C** *Tortaxis lubricus*, holotype ANSP 66056 from near Haiphong **D** *Tortaxis papillosa*, MNHN-IM-2000-33971 from Nam-Nhang **E** *Tortaxis permira*, syntype MNHN-IM-2000-4675 from That-Khé, Tonkin **F** *Tortaxis pilsbryi*, syntype MNHN-IM-2000-4678 from Bac-Khan et That-Khé **G–I** *Tortaxis cylindrotis* sp. nov. **G** holotype CUMZ 13078 from Taunggyi, Shan State, Myanmar with embryonic whorls and aperture **H, I** paratypes CUMZ 13079 from the type locality **H** probably juvenile shell with 7 whorls and **I** adult shell. Photographs: P Bourguignon & D Brabant (**B, D–F**).

The genus is mainly distributed in Southeast Asia and southern China and comprises 14 extant species (Pilsbry 1906; Schileyko 1999; MolluscaBase 2023) and one Miocene-amber fossil from China (Yu et al. 2023). In Indochina, nine species have been reported from Vietnam, and only one species from

Thailand (Panha 1998; Schileyko 2011; Do and Do 2014). In this study, we propose one new species which marks the first record of the genus in Myanmar.

38 *Tortaxis cylindropsis* Man & Panha, sp. nov.

https://zoobank.org/084E4BD5-300A-4391-AF52-A6A8F6ADD951
Fig. 16G–I, Table 1

Type specimens. ***Holotype*** CUMZ 13079 (height 9.6 mm, width 2.3 mm; Fig. 16G), ***paratypes*** CUMZ 13080 (35 shells; Fig. 16H, I), NHMUK 20230919 (2 shells) and SMF (2 shells).

Type locality. Parpant area, Taunggyi City, Taunggyi District, Shan State, Myanmar (20°15'3.7"N, 97°14'23.9"E).

Etymology. The specific name *cylindropsis* is from the Latin word for cylinder, and the Greek suffix *-opis* means ‘having the appearance of or like’. It refers to the cylindrical shell shape of this species.

Diagnosis. Shell slender cylindrical, suture deeply impressed, spire distinctly turreted, protoconch rounded and smooth, subsequent whorls with fine growth lines and a distinct spiral fold on columellar margin.

Description. Shell (height 9.3–11.7 mm) slender cylindrical in shape,, translucent, whitish to pale yellowish colour, and with 8–9½ whorls. Apex rounded; protoconch ~ 2 whorls, rounded and with smooth surface; subsequent whorls with fine growth lines more distinct on last whorl. Spire high, grows evenly and is largely turreted; whorls flatly convex; last whorls slightly larger than preceding whorls; suture narrow, deep, and weakly crenulated. Aperture vertical, narrowly ovate, and elongate; peristome thin; columella straight; columellar margin slightly expanded with distinct spiral fold. Umbilicus closed.

Distribution. This species is known only from its type locality.

Differential diagnosis. Comparing this new species with the Vietnamese species, *T. comaensis* Do, 2014 has a much larger and taller shell (height 56.1–66.4 mm), an attenuated spire, coarser sculptures, a broad aperture, and a thickened peristome, whereas this new species display a much smaller shell (height 9.3–11.7 mm), grows evenly and has a cylindrical spire, smooth shell surface, narrow aperture, and thin peristome (Do and Do 2014). *Tortaxis erectus* (Benson, 1842) has a less turreted shell, wide and flatly convex whorls, and a shallow suture (Fig. 16A), while *T. cylindropsis* sp. nov. has a distinctly turreted, slender shell with narrow and convex whorls, and a deep suture. *Tortaxis elongatissimus* Bavay & Dautzenberg, 1909 possesses a more elongated shell with stronger radial ribs and a more attenuated spire (Fig. 16B) than this new species. *Tortaxis lubricus* Pilsbry, 1906 has a broad last whorl, attenuated spire, wider aperture, and shallow suture (Fig. 16C); in contrast, the shell of *T. cylindropsis* sp. nov. presents narrowly and even whorls, cylindrical, slender, and turreted spire, narrow aperture, and deep suture. *Tortaxis papillosa* Dautzenberg & Fischer, 1908 shows a broad shell with an attenuated spire, rounded embryonic whorls, flatter whorls, and a shallow suture (Fig. 16D), whereas *T. cylindropsis* sp. nov. has a slender shell, with cylindrical spire, convex whorls, and deeper suture. *Tortaxis permira* (Ancey in Bavay & Dautzenberg, 1904) and *T. pilsbryi* (Ancey in Bavay & Dautzenberg, 1904) have a wider shell, with a shallower suture, gradually attenuated spire, and an aperture wider than that of *T. cylindropsis* sp. nov. (Fig. 16E, F).

Remarks. This genus is reported for the first time in Myanmar, and the present finding expands the distribution range of the genus from China, Vietnam, Laos, and Thailand to include Myanmar.

Genus *Zootecus* Westerlund, 1887

Zootecus Westerlund, 1887: 75. Kobelt 1902: 1022, 1032. von Martens 1895: 103. Pilsbry 1906: 104. Gude 1914: 366. Zilch 1959: 355. Schileyko 1999: 519, fig. 678. Neubert 2003: 154.
Obeliscella—Jousseaume, 1889: 359.
Chilogymnus—Jousseaume, 1894: 289.

Type species. *Pupa insularis* Ehrenberg, 1831, subsequent designation by Kobelt (1902: 1022).

Diagnosis. Shell pupiform; spire high, broad, cylindrical, and apex pointed; embryonic whorls smooth surface; subsequent whorls with irregularly dense, fine, coarse, or weak radial striations. Aperture oblique, broad, and oblong or rounded; columella straight. Penis long slender tube, and with slightly thickened wall and conical at base; vagina very much larger and muscularly thicker than male organ.

Remarks. *Zootecus* can be distinctly distinguished from all subulinid taxa in Myanmar by its pupiform shell, broad spire, straight columella, thickened whitish peristome, and irregular coarse striations (Table 2).

The genus is distributed from the Cabo Verde Islands and the Sahara, extending eastwards to Arabia, Socotra Island, India, and Southeast Asia (Gude 1914; Solem 1966; Schileyko 1999; Neubert 2003). Currently, the genus consists of nine species, and two are known from Myanmar (Gude 1914; MolluscaBase 2023).

39 *Zootecus insularis* (Ehrenberg, 1831)
Fig. 17A–C

Pupa insularis Ehrenberg, 1831: 13. Type locality: In insula Cameran, quae prope Maris rubri ostium australe inter Loheiam et Moccham iuxta Arabiae felicis littus sita est [Cameran Island, Red Sea between Loheia and Mocha, near coast of Arabia]. Pfeiffer 1848: 307.
Bulimus insularis—Pfeiffer 1853: 403. Hanley and Theobald 1870: 11, pl. 22, fig. 10.
Pupa (*Cylindrus*) *insularis*—Nevill 1877: 22.
Stenogyra insularis—von Martens 1895: 106, pl. 8, figs 5, 6.
Zootecus insularis—Pilsbry 1906: 106–108, pl. 26, figs 21–25, 29–33. Gude 1914: 367, 368. Schileyko 1999: 519, 520, fig. 678. Neubert 2003: 154, 155, figs 1, 2. Raheem et al. 2014: 118, fig. 74c.

Type specimen. ***Lectotype*** ZMB 109990 (Fig. 17A, after Raheem et al. 2014: fig. 74c).

Other material. NHMUK 1875.12.4.16 (5 shells; Fig. 17B, C) ex. Beddome collection from Burma. SMF 296651/2 (2 shells) ex. Ehrmann collection from Burma.

Diagnosis. Shell subcylindrical; spire high and dome-shaped; apex pointed; subsequent whorls with fine and wavy radial striae, which stronger near suture. Aperture semi-ovate; columella short and straight. Umbilicus narrow.

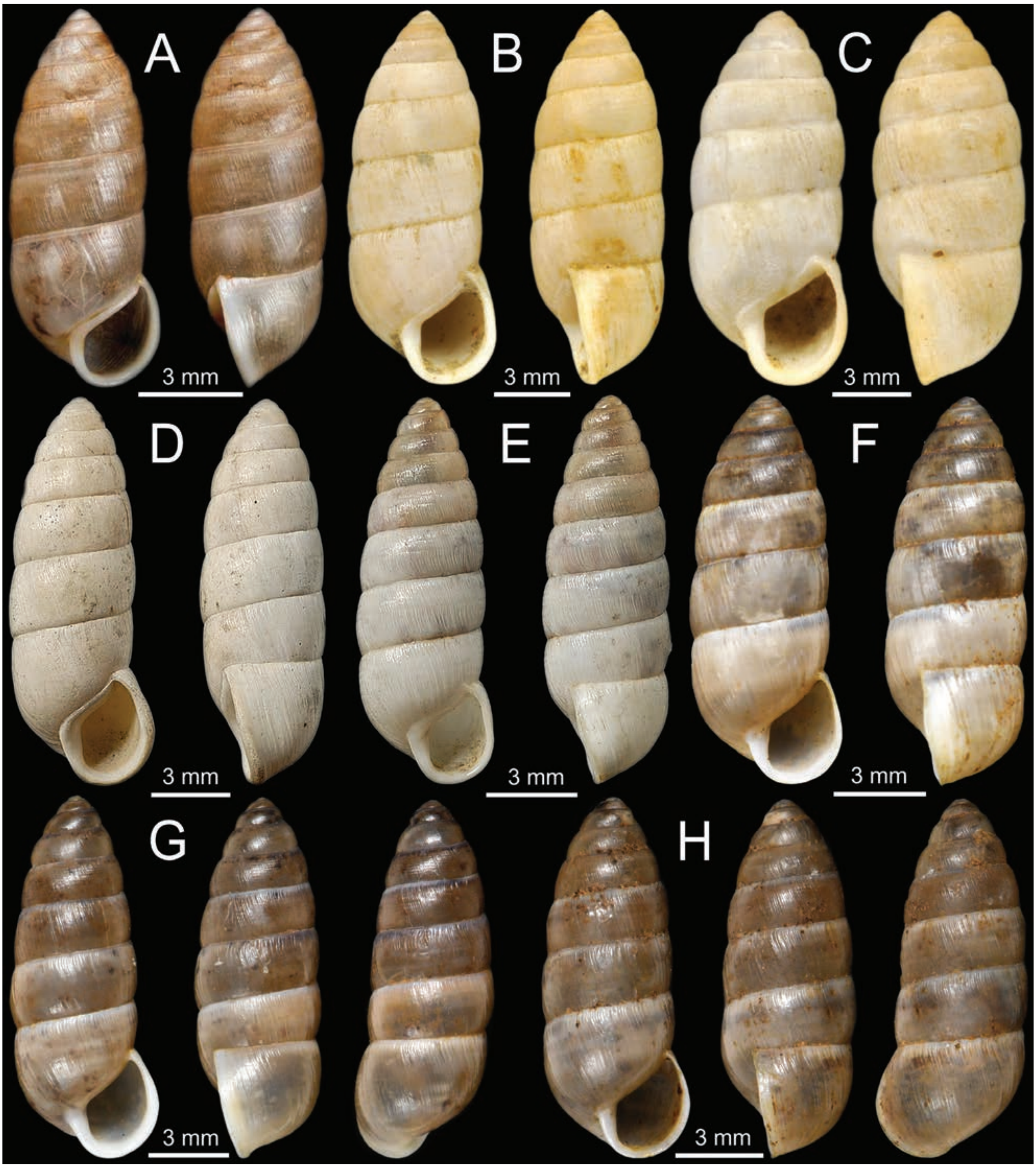


Figure 17. A–C *Zootecus insularis* **A** lectotype ZMB 109990 (after Raheem et al. 2014: fig. 74c) and **B, C** specimen NHMUK 1875.12.4.16 from Burma **D–H** *Zootecus pullus* **D** lectotype NHMUK 1986252/1 and **E** paralectotype NHMUK 1986252/2 from Banks of the Ganges, South Asia and **F–H** specimen CUMZ 13081 from Bagan, Mandalay Region, Myanmar.

Distribution. *Zootecus insularis* has a wide geographic distribution, spanning across the Cape Verde Islands, northeastern Africa, and the Arabian Peninsula. Its range also extends to South Asia, including India, Pakistan, Sri Lanka, and Afghanistan (Pilsbry 1906; Gude 1914; Neubert 2003; Raheem et al. 2014). In Myanmar, it was recorded from 'Pagan' [Bagan] in the Mandalay Region (Blanford 1865; Gude 1914).

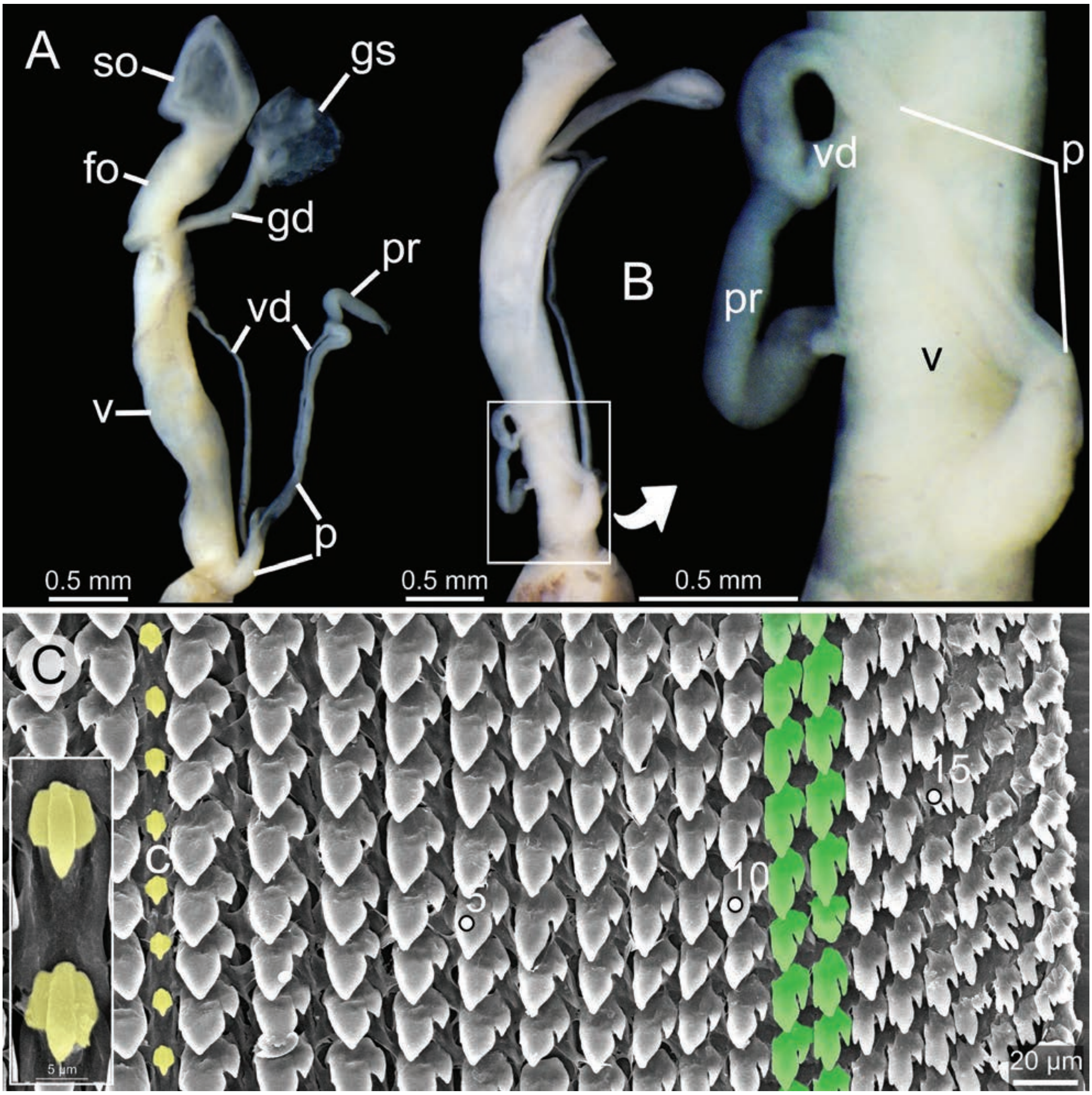


Figure 18. Genitalia and radula of *Zootecus pullus*, specimen CUMZ 13082 from Bagan, Mandalay Region, Myanmar **A, B** reproductive anatomy with inset of the male organ and **C** radula morphology with inset of central teeth: yellow colour and 'C' indicates central teeth row, green colour indicates lateral teeth in the transition to marginal teeth, and numbers indicate tooth order from lateral to marginal end. Abbreviations: **fo**, free oviduct; **gd**, gametolytic duct; **gs**, gametolytic sac; **p**, penis; **pr**, penial retractor muscle; **so**, spermoviduct; **v**, vagina; **vd**, vas deferens.

Remarks. No new specimens of this species were collected during this survey. However, the specimens collected from Bagan in the Mandalay Region are here identified as *Z. pullus* rather than *Z. insularis* (see under *Z. pullus* for further comparison). The historical museum specimens with brief locality records such as 'Burma' (Fig. 17B, C) match well with the respective type specimens of this species (Fig. 17A). As a result, the existence of *Z. insularis* in Myanmar requires further evidence from newly collected specimens with precise collection locality data, otherwise it must be excluded from the faunal list.

40 *Zootecus pullus* (Gray, 1834)

Figs 17D–H, 18, Table 1

Bulimus pullus Gray, 1834: 66. Type locality: India Orientali ad ripas Gangis [Eastern India, banks of the Ganges River]. Pfeiffer 1848: 162. Reeve 1849b: *Bulimus* pl. 67, species 476. Blanford 1865: 94.
Bulimus (*Opeas*) *pullus*—Albers 1850: 175.
Pupa (*Cylindrus*) *pulla*—von Martens 1860: 297.
Bulimina (*Mastus*) *pulla*—Pfeiffer and Clessin 1881: 293.
Rumina pulla—Ancey 1886: 61.
Stenogyra pulla—von Martens 1895: 106, 107, pl. 8, figs 7, 8.
Zootecus insularis var. *pullus*—Pilsbry 1906: 110, pl. 26, figs 26–28.
Zootecus pullus—Gude 1914: 371, 372. Raheem et al. 2014: 118, 119, fig. 74e, f.

Type specimens. ***Lectotype*** NHMUK 1986252/1 (Fig. 17D; designated in Raheem et al. 2014). ***Paralectotype*** NHMUK 1986252 (1 shell; Fig. 17E) from Banks of the Ganges, South Asia.

Other material. Dhammayazaka Pagoda, Pwasaw Village, Bagan City, Mandalay Region, Myanmar (21°08'40.3"N, 94°52'58.0"E): CUMZ 13081 (70 shells; Fig. 17F–H), CUMZ 13082 (20 specimens in ethanol).

Description. Shell subcylindrical, solid, glossy, pale grey colour, slightly thick, and with 8–9½ whorls. Apex slightly elevated; protoconch ~ 2 whorls, dome-shaped and nearly smooth with fine radial striations; subsequent whorls with dense but fine, wavy, radial striations, stronger near suture. Spire grows evenly; whorls flatly convex; suture wide and shallow. Aperture nearly rounded and wide; columella straight; peristome relatively thickened, expanded, and white. Umbilicus narrowly opened.

Genitalia (*n* = 5). Atrium undifferentiated. Penis very narrow, slender, almost same length with vagina, and slightly bulging at base. Penial retractor slender, long and attached at junction of penis and vas deferens. Epiphallus very short or indistinct. Vas deferens long, slender tube, and connected between penis/epiphallus to free oviduct (Fig. 18A, B).

Vagina much larger than penis and cylindrical shape. Gametolytic duct short and slender tube; gametolytic sac distinct and bulbus shape. Free oviduct almost the same diameter as vagina; spermoviduct enlarged.

***Radula*.** Each row contains ~ 43+ teeth with half-row formula: central-lateral-marginal teeth (1–(11–13)–(6–7+)). Central tooth relatively small, tricuspid with pointed central cusp, and small, rounded, lateral cusps. Lateral teeth bicuspid: endocone large rhomboid in shape and with pointed to dull tip; ectocone small, pointed tip and located at middle of tooth height. Marginal teeth asymmetrically tricuspid starting approximately at tooth number 11–13: mesocone large, triangular, and curved to blunt tip; endocone small and located near tip of mesocone; ectocone triangular, pointed tip and located near tooth base. Outermost teeth small and polycuspid (Fig. 18C).

Distribution. Apart from Myanmar, this species is likely to occur in India and Bangladesh (Raheem et al. 2014).

Remarks. In Myanmar, the previous records of *Z. pullus* were from 'Ava' [Innwa in Mandalay Region]. Our newly collected specimens from Bagan (~ 150 km southwest of Innwa) are identified as this species, but they present some differences such as having a long and narrower shell and a blunt apex. *Zootecus* *pullus* has a penis nearly equal in length to the vagina, and the penis is slightly enlarged with a conical shape at base near the atrium (Fig. 18A, B), while *Z. insularis* possesses a penis shorter than the vagina, and the evenly slender penis (see Schileyko 1999: fig. 678 from a near type locality in the Red Sea). Further investigation is required to determine whether these two Myanmar species are distinct or simply demonstrate variation in shell morphology.

Conclusions

This study elucidates the historically known species of the Subulinidae in Myanmar, identifying nine genera and 40 taxa, including 2 newly described species. Of these, 17 species are restricted only to Myanmar, while the remaining species are also found in India, China, and other Southeast Asian countries. The genera *Glessula* and *Rishetia* represent the highest number of species, 12 and 10 species, respectively, and they are predominantly found in Myanmar rather than other countries in Indochina. The globally distributed *Allopeas gracile* and the newly described species *Tortaxis cylindropsis* sp. nov. are presently documented as the only species of these genera in Myanmar.

Except for *Opeas innocens*, all other unique name-bearing types of the subulinid species recorded from Myanmar have been examined, revised, and are illustrated herein. Our revised taxonomy is grounded in literature records; however, the classification of one particular taxa that has never been illustrated or for which there are no available types remains somewhat arbitrary. Additionally, in regards to the distribution range of certain species, for instance e.g., *G. crassilabris*, *G. orophila*, and *R. hastula*, which extend well beyond their original type locality in India, further data is needed to confirm their occurrence in Myanmar.

The distribution of these subulinid snails sheds light on their historical prevalence. According to the literature, they are primarily found in regions such as Bago, Ayeyarwady, Magway, Rakhine, and Shan rather than in Mon and Kayin states, which are known for their rich limestone outcrops (Gude 1914; Godwin-Austen 1920). Species belonging to the genera *Glessula*, *Opeas*, *Paropeas*, *Tortaxis*, and *Zootecus* were collected in Shan State, Mandalay, and Tanintharyi regions. However, our recent survey did not encounter representative taxa for *Bacillum*, *Curvella*, and *Rishetia*. Instead, species like *Paropeas turricula* and *Opeas filiforme* have expanded their distribution from Thailand into Myanmar, and the genus *Tortaxis* is recorded for the first time. In contrast, other families like Ariophantidae (Pholyotha et al. 2020; Sutcharit and Pholyotha 2023), Clausiliidae (Man et al. 2023), Helicarionidae (Sutcharit et al. 2020a; Pholyotha et al. 2022a, b), Hypselostomatidae (Tongkerd et al. 2024), and Streptaxidae (Man et al. 2022) have yielded several species in Mon and Kayin states during these surveys. Hence, subsequent surveys should focus on regions such as Bago, Ayeyarwady, Magway, and Rakhine, aiming to confirm the identity of uncertain species and to undertake a thorough revision using freshly collected material. Moreover, the occurrence of new records suggests that additional taxa are likely to be discovered.

Budha et al. (2017) highlighted that shell sculptures may serve as valuable characters in distinguishing *Glessula* and *Rishetia*. Likewise, our limited new sample of *Glessula* demonstrates a range of shell surface variations from smooth to ribbed sculpture. Species like *G. mandalayensis* sp. nov. and

G. gemma exhibit smooth to fine striations, while grooves are observed in *G. feddeni* and *G. latestriata*, and ribbed sculpture is characteristic of *G. blanfordiana*. Similarly, *Paropeas* is characterised by rough and compact radial striations, while *Allopeas* has finer striations compared to *Paropeas*. On the other hand, *Opeas* and *Tortaxis* display the very fine striations or smooth surfaces among these two genera. However, future research in subulinid taxonomy still requires the integration of genetic data, genital anatomy, and shell morphological traits for a more comprehensive understanding of their systematics.

Acknowledgements

The senior author is grateful to all members of the Animal Systematics Research Unit (ASRU), Chulalongkorn University, for their kind help during field trips in Myanmar. The authors are indebted to V Héros, P Bourguignon, and D Brabant (project ERECOLNAT: ANR-11-INBS-0004, MNHN, Paris); K Webb and H Taylor (NHMUK, London), R Janssen, J. Sigwart, K-O Nagel, and S Hof (SMF, Frankfurt), and B Páll-Gergely (Centre for Agricultural Research, Budapest) for kindly providing the authors with the shell photographs of material housed in their type collections. We thank the personnel of the Apache Cement Company for sponsoring our surveys in the Mandalay Region. We also thank the Ministry of Natural Resources and the Environmental Conservation Forest Department, Myanmar, for the collection and export permits. We also thank DJ Anderson for his initial linguistic help in the original manuscript. We gratefully acknowledge the reviewers, F Naggs, B Páll-Gergely, JK Foon, S D'ávila and an anonymous reviewer for their helpful and constructive comments, which significantly improved the manuscript.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

The work in Thailand was funded by the Thailand Research Fund (TRF-DPG628001), the NSRF via the Program Management Unit for Human Resources & Institutional Development, Research and Innovation (B42G670038), National Research Council of Thailand (NRCT-N35E660138) and Centre of Excellence on Biodiversity (MHESI), and additional support by CU-ASEAN Scholarships and the 90th Anniversary of Chulalongkorn University Fund to NSM. The field trips in Myanmar were partially funded through grants received from Fauna and Flora International (FFI) and Thailand Research Fund (TRF-RTA 5880002).

Author contributions

NSM, NL, CS, and SP collected and prepared specimens in the field. NL, CS, and SP provided financial and intellectual support. NSM and CS prepared specimens and wrote the manuscript. NSM and CS conceived, designed, supervised the study, prepared figures, and approved and edited the final manuscript. JDA reviewed, advised, and approved the final manuscript.

Author ORCIDs

Nem Sian Man https://orcid.org/0000-0002-4453-734X
Jonathan D. Ablett https://orcid.org/0000-0002-7277-1934
Ngwe Lwin https://orcid.org/0000-0002-4394-3741
Chirasak Sutcharit https://orcid.org/0000-0001-7670-9540
Somsak Panha https://orcid.org/0000-0002-4431-2458

Data availability

All of the data that support the findings of this study are available in the main text.

References

Adams H, Adams A (1855) [1854–1858] The Genera of Recent Mollusca; Arranged According to their Organization. Volume 2. van Voorst, London, 661 pp. [pp 93–284 (1855)]

Albers JC (1850) Die Heliceen nach natürlicher Verwandtschaft systematisch geordnet. Enslin, Berlin, 262 pp. https://doi.org/10.5962/bhl.title.11507

Albers JC (1860) Die Heliceen nach Natürlicher Verwandtschaft Systematisch Geordnet, 2nd edn. (manuscript edited by E. von Martens). Wilhelm Englemann, Leipzig, 359 pp. https://doi.org/10.5962/bhl.title.11218

Ancey CF (1886) Esssai monographique sur le *Buliminus* de l'Asie Centrale Russe et de l'Afghanistan. Bulletin de la Société Malacologique de France 3: 15–64.

Baker HB (1935) Jamaican land snails, 3. The Nautilus 48(3): 83–88. https://doi.org/10.5962/bhl.part.11532

Bavay A, Dautzenberg P (1904) Description de coquilles nouvelles de l'Indo-Chine. (3e suite). Journal de Conchyliologie 51[1903]: 201–236.

Bavay A, Dautzenberg P (1909) Molluscorum terrestrum tonkinorum diagnoses. Journal de Conchyliologie 56[1908]: 229–251. https://www.biodiversitylibrary.org/page/16298225

Beddome CR (1906) Notes on Indian and Ceylonese species of *Glessula*. The Journal of Molluscan Studies 6(3): 160–172. https://doi.org/10.1093/oxfordjournals.mollus.a066160

Benson WH (1836) Descriptive catalogue of terrestrial and fluviatile Testacea, chiefly from the North-East frontier of Bengal. Journal of the Asiatic Society of Bengal 5(54): 350–358. https://biodiversitylibrary.org/page/37188459

Benson WH (1842) Mollusca. In: T. Cantor, General features of Chusan, with remarks on the flora and fauna of that island. Annals and Magazine of Natural History, Series 1 9(60): 486–490. https://www.biodiversitylibrary.org/page/18684698

Benson WH (1857) New species of *Bulimus* from India, Burma, and Mauritius. Annals & Magazine of Natural History Series 2 19(112): 327–330. https://doi.org/10.1080/00222935708693934

Benson WH (1860) On new land-shells from Darjiling, with a series of new Indian species of Achatina. Annals & Magazine of Natural History Series 3 5(30): 460–466. https://doi.org/10.1080/00222936008697255

Benson WH (1863) Characters of new land-shells from the Andaman Islands, Burmah, and Ceylon, and of the animal of *Sophina*. Annals & Magazine of Natural History Series 3 11(65): 318–323. https://doi.org/10.1080/00222936308681435

Benson WH (1865) New land-shells from Travancore, western and northern India. Annals & Magazine of Natural History Series 3 15(85): 11–15. https://doi.org/10.1080/00222936508681753

Blanford WT (1861) Contributions to Indian malacology, No. II. Journal of the Asiatic Society of Bengal 30(4): 347–366. https://www.biodiversitylibrary.org/item/207709

Blanford WT (1865) Contributions to Indian Malacology, No. 5. Description of new land shells from Arakan, Pegu, and Ava; with notes on the distributions of described species. Journal of the Asiatic Society of Bengal 34(2): 66–105. https://www.biodiversitylibrary.org/item/114408

Blanford WT (1869) Descriptions of new land and freshwater molluscan species collected by Dr. John Anderson in Upper Burma and Yunnan. Proceedings of the Zoological Society of London 37(1): 444–450. https://doi.org/10.1111/j.1469-7998.1869.tb07354.x

Blanford WT (1871) On some undescribed species of *Camptoceras* and other land shells. Journal of the Asiatic Society of Bengal 40: 39–45. https://www.biodiversitylibrary.org/page/35630849

Blanford WT (1903) Notes on Mr. WM Daly's collections of land and fresh-water Mollusca from Siam. Proceedings of the Malacological Society of London 5(4): 274–284. https://doi.org/10.1093/oxfordjournals.mollus.a065982

Bouchet P, Rocroi JP, Hausdorf B, Kaim A, Kano Y, Nützel A, Strong EE (2017) Revised classification, nomenclator and typification of gastropod and monoplacophoran families. Malacologia 61(1–2): 1–526. https://doi.org/10.4002/040.061.0201

Bourguignat J-R (1883) Histoire malacologique de l'Abyssinie. Annales des Sciences Naturelles (Zoologie et Paléontologie) (6)15(2): 1–162. https://www.biodiversitylibrary.org/bibliography/46223#/summary

Budha PB (2017) First record of *Curvella sikkimensis* (Reeve, 1850) (Pulmonata: Subulinidae: Subulininae) from Nepal and its reproductive organs. Nepalese Journal of Biosciences 7(1): 120–124. https://doi.org/10.3126/njbs.v7i1.41801

Budha PB, Naggs F, Backeljau T (2015) Annotated checklist of the terrestrial gastropods of Nepal. ZooKeys 492: 1–48. https://doi.org/10.3897/zookeys.492.9175

Budha PB, Naggs F, Backeljau T (2017) Conchological differentiation and genital anatomy of Nepalese Glessulinae (Gastropoda, Stylommatophora, Subulinidae), with descriptions of six new species. ZooKeys 675: 129–156. https://doi.org/10.3897/zookeys.675.13252

Chaper M (1885) Description de quelques espèces et genres nouveaux de coquilles vivantes de diverses provenances. Bulletin de la Société Zoologique de France 10: 42–54. https://doi.org/10.5962/bhl.part.14302

D'ávila S, Medeiros C, Vargas T, Mendonça CLF (2018) Life history of *Subulina octona* (Brugüière) (Gastropoda: Pulmonata: Subulinidae) based on four-year laboratory observations and a comparative histological analysis of egg-retaining and ovoviviparous subulinids. Journal of Natural History 52(23–24): 1551–1569. https://doi.org/10.1080/00222933.2018.1478996

D'ávila S, Simone LRL, De Oliveira LFC, Charles L, Maestrati P (2020) Rediscovery of *Obeliscus agassizi* Pilsbry, 1906 (Gastropoda, Subulinidae, Obeliscinae), annotated checklist of species of *Obeliscus* Beck, 1837 and first description of the anatomy for the genus. Zoosystema 42(12): 159–172. https://doi.org/10.5252/zoosystema20v42a12

Dautzenberg P, Fischer H (1908) Liste des mollusques récoltés par M. Mansuy en Indo-Chine et description d'espèces nouvelles. Journal de Conchyliologie 56: 169–217.

de Morgan J (1885) Mollusques terrestes et fiuviatiles de Royaume de Perak et des pais voisins (presque'Ile Malaise). Bulletin de la Société Zoologique de France 10: 353–429. https://doi.org/10.5962/bhl.part.14301

Do DS, Do VN (2014) The land snail family Subulinidae (Gastropoda: Pulmonata) from Sonla, Vietnam, with description of two new species. Tapchi Sinh Hoc 36(11): 451–459. https://doi.org/10.15625/0866-7160/v36n4.6174

Ehrenberg CG (1831) Animalia evertebrata. Symbolae physicae seu icones et descriptiones naturalium novorum aut minus cognitorum quae ex itineribus Lybiam Aegyptum

Nubiam Dongalam Syriam Arabiam et Habessinian. Pars Zoologica. Abhandlungen der deutschen Akademie der Wissenschaften. 4: (unpaginated). https://www.biodiversitylibrary.org/page/48517192

Férussac AE d'Audebard de baron de (1821) [1821–1822] Tableaux systématiques des animaux mollusques suivis d'un Prodrome général pour tous les mollusques ou fluviatiles, vivantes ou fossiles, 114 pp. [pp 1–114 (1821); pp i–xlvii (1822)] https://www.biodiversitylibrary.org/bibliography/10558

Fischer P, Crosse H (1877) Études sur les mollusques terrestres et fluviatiles du Mexique et du Guatemala. Mission scientifique au Mexique et dans l'Amerique Centrale. Recherches Zoologiques, Partie 7, Volume 1, 702 pp. https://www.biodiversitylibrary.org/item/216870

Fontanilla IK, Naggs F, Wade CM (2017) Molecular phylogeny of the Achatinoidea (Mollusca: Gastropoda). Molecular Phylogenetics and Evolution 114: 382–385. https://doi.org/10.1016/j.ympev.2017.06.014

Foon JK, Clements GR, Liew TS (2017) Diversity and biogeography of land snails (Mollusca, Gastropoda) in the limestone hills of Perak, Peninsular Malaysia. ZooKeys 682: 1–94. https://doi.org/10.3897/zookeys.682.12999

Godwin-Austen (1876) On the Helicidae collected during the expedition into the Dafla Hills, Assam. Journal of the Asiatic Society of Bengal 45(4): 311–184. https://www.biodiversitylibrary.org/item/114186

Godwin-Austen HH (1895) List and distribution of the Land-Mollusca of the Andaman and Nicobar Islands, with descriptions of some supposed new species. Proceedings of the Zoological Society of London 63(30): 438–457. https://www.biodiversitylibrary.org/page/30983429

Godwin-Austen HH (1918) Zoological results of the Abor Expedition, 1911–1912. XLIX. Mollusca, IX. Records of the Indian Museum 8(12): 601–621. https://doi.org/10.26515/rzsi/v8/i12/1918/163139

Godwin-Austen HH (1920) Land and freshwater Mollusca of India, including South Arabia, Baluchistan, Afghanistan, Kashmir, Nepal, Burmah, Pegu, Tenasserim, Malay Peninsula, Ceylon, and other islands of the Indian Ocean. Supplementary to Messrs. Theobald and Hanley's Conchologia Indica. London, Taylor & Francis, Volume 3, 1–65. [pls 159–165] https://www.biodiversitylibrary.org/item/57585

Gray JE (1834) Exhibition of an extensive series of land and freshwater shells regarded as hitherto undescribed. Proceedings of the Zoological Society of London 2: 63–68. https://biodiversitylibrary.org/page/12859659

Gray JE (1860) On the arrangement of the land pulmoniferous Mollusca into familie. Annals & Magazine of Natural History Series 3 6(34): 267–269. https://doi.org/10.1080/00222936008697321

Gude GK (1914) Mollusca-II. Trochomorphidae-Janellidae. In: Shipley AE, Marshall GAK (Eds) The Fauna of British India, including Ceylon and Burma. Taylor & Francis, London, 520 pp. https://doi.org/10.5962/bhl.title.12891

Hanley SCT, Theobald W (1870, 1873, 1874) [1870–1876] Conchologia Indica: Illustrations of the Land and Freshwater Shells of British India. London, 1–65. [pls 1–160] [pp 1–18, pls 1–40 (1870); pp 19–28, pls 41–60 (1872); pp 29–34, pls 61–80 (1873). pp 35–48, pls 81–120 (1874); pp 49–56, pls 121–140 (1875); pp 57–65, pls 141–160 (1876)] https://www.biodiversitylibrary.org/item/50391

Horsák M, Naggs F, Backeljau T (2020) *Paropeas achatinaceum* (Pfeiffer, 1846) and other alien Subulinine and Opeatine land snails in European greenhouses (Gastropoda, Achatinidae). Malacologia 63(1): 123–130. https://doi.org/10.4002/040.063.0112

Hutton T (1834) On the land shells of India. Journal of the Asiatic Society of Bengal 3(26): 81–93.

Illiger JCW (1801) Namen der Insekten-Gattungen, ihr Genitiv, ihr grammatisches Geschlecht, ihr Silbenmass, ihr Herleitung; zugleich mit den Deutschen Benennungen. Magazin für Insektenkunde 1: 125–155.

Inkhavilay K, Sutcharit C, Bantaowong U, Chanabun R, Siriwut W, Srisonchai R, Pholyotha A, Jirapatrasilp P, Panha S (2019) Annotated checklist of the terrestrial molluscs from Laos (Mollusca, Gastropoda). ZooKeys 834: 1–166. https://doi.org/10.3897/zookeys.834.28800

International Commission on Zoological Nomenclature (ICZN) (1999) International Code of Zoological Nomenclature (4th edn.) International Trust for Zoological Nomenclature, London, 306 pp.

Jaeckel S (1950) Die Mollusken eines tropischen Flußgenistes aus Tonkin. Archiv für Molluskenkunde 79: 15–20.

Jousseaume F (1889) Espèces nouvelles des environs d'Aden suivies d'un aperçu sur la faune malagologique de la Péninsule Arabique. Bulletins de la Société Malacologique de France 6: 345–362. https://www.biodiversitylibrary.org/page/16141631

Jousseaume F (1894) Mollusques recueillis à Ceylan par M.E. Simon, et révision générale des espèces terrestres et fluvio-lacustres de cette ile. Mémoires de la Société Zoologique de France 7: 264–330. https://www.biodiversitylibrary.org/page/36340927

Kalita G (2022) Land snails of Guwahati, Assam, India. Journal of Threatened Taxa 14(9): 21845–21852. https://doi.org/10.11609/jott.8019.14.9.21845-21852

Kerney MP, Cameron RAD (1979) A Field Guide to the Land Snails of Britain and Northwest Europe. Collins, London.

Kobelt W (1901, 1902) [1899–1902] Die Familie Buliminidae. In: Systematisches Conchylien-Cabinet von Martini und Chemnitz 1, 13(2): 397–1051. [pls 71–133] [pp 397–620, pls 71–94 (1899); pp 621–684, pls 95–103 (1900); pp 685–836, pls 104–123 (1901); pp 837–1051, pls 124–133 (1902)] https://www.biodiversitylibrary.org/item/106746

Laidlaw FF (1933) A list of the land and fresh-water Mollusca of the Malay Peninsula. Journal of the Malaysian Branch of the Royal Asiatic Society 11: 211–234.

Lamouroux JVF (1816) Histoire des Polypiers Coralligènes Flexibles, Vulgairement Nommés Zoophytes. F. Poisson, Caen, 558 pp. https://www.biodiversitylibrary.org/page/11606092

Maassen WJM (2001) A preliminary checklist of the non-marine molluscs of West Malaysia. De Kreukel 2001: 1–155.

Man NS, Siriboon T, Lin A, Sutcharit C, Panha S (2022) Revision of the carnivorous land snail family Streptaxidae (Stylommatophora, Achatinina) in Myanmar, with description of four new species. ZooKeys 1110: 39–102. https://doi.org/10.3897/zookeys.1110.85399

Man NS, Lwin N, Sutcharit C, Panha S (2023) Further notes on the taxonomy of the land snail family Clausiliidae Gray, 1855 (Stylommatophora, Helicina) from Myanmar with description of two new species. ZooKeys 1160: 1–59. https://doi.org/10.3897/zookeys.1160.98022

Miller JS (1822) A list of the freshwater and landshells occurring in the environment of Bristol, with observations. Annals of Philosophy, New Series 3(5): 376–381. https://www.biodiversitylibrary.org/page/2498134

MolluscaBase eds (2023) MolluscaBase. https://www.molluscabase.org [in 2023–07–17] https://doi.org/10.14284/448

Mörch OAL (1876) Revision des mollusques terrestres des iles Nicobar. Journal de Conchyliologie 24: 353–367. https://www.biodiversitylibrary.org/page/16071668#page/375

Morlet L (1893) Descriptions d'espèces nouvelles provenant de l'Indochine. Journal de Conchyliologie 40[1892]: 315–329.

Mousson A (1857) Novitates Zollingerianae (1). Journal de Conchyliologie 6(2): 154–164.

Naggs F (1994) The reproductive anatomy of *Paropeas achatinaceum* and a new concept of *Paropeas* (Pulmonata: Achatinoidea: Subulinidae). The Journal of Molluscan Studies 60(2): 175–191. https://doi.org/10.1093/mollus/60.2.175

Neubert E (2003) The continental malacofauna of Arabia and adjacent areas. II. The genus *Zootecus* Westerlund, 1887. Archiv für Molluskenkunde der Senckenbergischen Naturforschenden Gesellschaft 132(1/2): 153–160. https://doi.org/10.1127/arch.moll/132/2003/153

Neubert E, Bochud E (2020) The continental malacofauna of Arabia and adjacent areas, VII. The family Achatinidae (Coeliaxinae, Subulininae) in the Socotran Archipelago (Gastropoda, Pulmonata). Rendiconti Lincei. Scienze Fisiche e Naturali 31(3): 655–676. https://doi.org/10.1007/s12210-020-00920-y

Nevill G (1877) List of the Mollusca brought back by Dr. J. Anderson from Yunnan and Upper Burma, with descriptions of new species. Journal of the Asiatic Society of Bengal 46(2): 14–41. https://www.biodiversitylibrary.org/item/110105

Nevill G (1878) Hand list of Mollusca in the Indian Museum, Calcutta. Part I. Gastropoda. Indian Museum, Calcutta, 338 pp. https://doi.org/10.5962/bhl.title.11957

Nevill G (1881) New or little-known Mollusca of the Indo-Malayan Fauna. Journal of the Asiatic Society of Bengal 50(2): 125–167. https://www.biodiversitylibrary.org/item/110180

Nurinsiyah AS, Hausdorf B (2019) Listing, impact assessment and prioritization of introduced land snail and slug species in Indonesia. The Journal of Molluscan Studies 85(1): 92–102. https://doi.org/10.1093/mollus/eyy062

Panha S (1998) A checklist and classification of the terrestrial pulmonate snails of Thailand. Walkerana 8[1995–1996](19): 31–40.

Pfeiffer L (1845) Diagnosen einiger neuer Heliceen. Zeitschrift für Malakozoologie 2: 152–158. https://biodiversitylibrary.org/page/16291740

Pfeiffer L (1846) Descriptions of nine new species of Helicea, collected by Hugh Cuming, Esq. Proceedings of the Zoological Society of London 14: 41–43.

Pfeiffer L (1848) Monographia Heliceorum Viventium: sistens descriptiones systematicas et criticas omnium huius familiae generum et specierum hodie cognitarum. Volumen Secundum. Lipsiae: F.A. Brockhaus, 594 pp. https://doi.org/10.5962/bhl.title.124010

Pfeiffer L (1853) Monographia Heliceorum Viventium: sistens descriptiones systematicas et criticas omnium huius familiae generum et specierum hodie cognitarum. Volumen Tertium. Lipsiae: F.A. Brockhaus, 711 pp. https://www.biodiversitylibrary.org/item/47349

Pfeiffer L (1856) Versuch einer Anordnung der Heliceen nach natürlichen Gruppen. Malakozoologische Blätter 2: 112–185. https://www.biodiversitylibrary.org/item/53876

Pfeiffer L (1859) Monographia Heliceorum Viventium: sistens descriptiones systematicas et criticas omnium huius familiae generum et specierum hodie cognitarum. Volumen Quartum. Lipsiae: F.A. Brockhaus, 920 pp. https://www.biodiversitylibrary.org/page/11648889

Pfeiffer L (1860) [1840–1865] [in HC Küster, L Pfeiffer] Die Bulimiden und Achatinen, In Abbildungen nach der Natur. Die gattungen *Bulimus*, *Partula*, *Achatinella*, *Achatina* und *Azeca*. In: Küster HC, Ed. Systematisches Conchylien-Cabinet von Martini und Chemnitz. Neu herausgegeben und vervollständigt. Erster Bandes, dreizehnte

Abtheilung. 1 (13) [(1, 124)]: iii–xix, 1–359. [pls 1–70] [pp 305–336 (1860), pls 25–29 (1863)] https://www.biodiversitylibrary.org/item/106739

Pfeiffer L (1868) Monographia Heliceorum Viventium: sistens descriptiones systematicas et criticas omnium huius familiae generum et specierum hodie cognitarum. Volumen Sextum. Lipsiae: F.A. Brockhaus, 598 pp. https://www.biodiversitylibrary.org/item/46666

Pfeiffer L (1876) [1876–1877] Monographia Heliceorum Viventium: sistens descriptiones systematicas et criticas omnium huius familiae generum et specierum hodie cognitarum. Volumen Octavum. Lipsiae: F.A. Brockhaus, 729 pp. [pp 1–480 (1876); pp 481–729 (1877)] https://www.biodiversitylibrary.org/item/47348

Pfeiffer L, Clessin S (1881) Nomenclator Heliceorum Viventium: quo continetur nomina omnium hujus familiae generum et specierum hodie cognitarum, disposita ex affinitate naturali. Kassel, Fischer, 617 pp. https://www.biodiversitylibrary.org/item/47266

Pholyotha A, Sutcharit C, Tongkerd P, Lin A, Panha S (2020) Taxonomic revision of the land snail genera *Macrochlamys* Gray, 1847 and *Sarika* Godwin-Austen, 1907 (Eupulmonata: Ariophantidae) from south-eastern Myanmar, with descriptions of three new species. Molluscan Research 40(2): 183–204. https://doi.org/10.1080/13235818.2020.1723041

Pholyotha A, Sutcharit C, Lin A, Panha S (2022a) Multigene phylogeny reveals the ribbed shell morphotypes in the land snail genus *Sarika* (Eupulmonata: Ariophantidae), with description of two new species from Thailand and Myanmar. Contributions to Zoology (Amsterdam, Netherlands) 91(2): 97–132. https://doi.org/10.1163/18759866-bja10027

Pholyotha A, Sutcharit C, Lin A, Panha S (2022b) Uncovering local endemism from southeastern Myanmar: Description of the new karst-associated terrestrial snail genus *Burmochlamys* (Eupulmonata, Helicarionidae). ZooKeys 1110: 1–37. https://doi.org/10.3897/zookeys.1110.82461

Pilsbry HA (1906) [1906–1907] Manual of Conchology, Structural and Systematic, with Illustrations of the Species, Series 2, Pulmonata. Volume 18: Achatinidae: Stenogyrinae and Coeliaxinae. Conchological Section, Academy of Natural Sciences of Philadelphia, Philadelphia, 1–357. [pls 1–51] [pp 1–272, pls 1–34 (1906); pp 273–357, pls 35–51 (1907)] https://doi.org/10.1175/1520-0493(1907)35%3C357a:LP%3E2.0.CO;2

Pilsbry HA (1908) [1908–1910] Manual of Conchology, Structural and Systematic, with Illustrations of the Species, Series 2, Pulmonata. Volume 20: Caecilioides, *Glessula* and Partulidae. Conchological Section, Academy of Natural Sciences of Philadelphia, Philadelphia, 1–336. [pls 1–43] [pp 1–64, pls 1–10 (1908); pp 65–314, pls 22–36 (1909); pp 315–336, pls 37–43 (1910)] https://www.biodiversitylibrary.org/item/16293

Preece RC, White TS, Raheem DC, Ketchum H, Ablett J, Taylor H, Naggs F (2022) William Benson and the golden age of malacology in British India: Biography, illustrated catalogue and evaluation of his molluscan types. Tropical Natural History (Supplement 6): 1–434.

Preston HB (1910) Description of new shells in the collection of the Indian Museum from Burma, Siam, and the Bay of Bengal. Records of the Indian Museum 5(1): 33–36. https://doi.org/10.26515/rzsi/v5/i1/1910/163757

Raheem DC, Taylor H, Ablett J, Preece RC, Aravind NA, Naggs F (2014) A systematic revision of the land snails of the Western Ghats of India. Tropical Natural History (Supplement 4): 1–294.

Ramakrishna, Mitra SC, Dey A (2010) Annotated checklist of Indian land molluscs. Occasional paper no. 306. Zoological Survey of India, 359 pp.

Rang S (1831) Description des coquilles terrestres recueillies pendant un voyage à la côte occidentale d'Afrique, et au Brésil. Annales des Sciences Naturelles 24(93): 5–63.

Reeve LA (1849a, 1850) [1849–1850] Conchologia Iconica: Illustrations of the shells of molluscous animals. Volume 5, Monograph of the genus *Achatina*, plates 1–23. Lovell Reeve and Co., London. [pls 1–19 (1849); pls 20–23 (1850)]. https://www.biodiversitylibrary.org/page/8967091

Reeve LA (1849b) [1848–1850] Conchologia Iconica: Illustrations of the shells of molluscous animals. Volume 5, Monograph of the genus *Bulimus*, plates 1–89. Lovell Reeve and Co., London. [pls 1–57 (1848); pls 58–84 (1849); pls 85–89 (1850)] https://www.biodiversitylibrary.org/item/35904

Schileyko AA (1999) Treatise on recent terrestrial pulmonate molluscs Part 4. Draparnaudiidae, Caryodidae, Macrocyclidae, Acavidae, Clavatoridae, Dorcasiidae, Sculptariidae, Corillidae, Plectopylidae, Megalobulimidae, Strophocheilidae, Cerionidae, Achatinidae, Subulinidae, Glessulidae, Micractaeonidae, Ferrussaciidae. Ruthenica (Supplement 2): 437–564.

Schileyko AA (2011) Checklist of land pulmonate molluscs of Vietnam (Gastropoda: Stylommatophora). Ruthenica 21(1): 1–68.

Schileyko AA, Kuznetsov AG (1996) A new genus of the Subulinidae (Pulmonata) from Nepal. Ruthenica 5(2): 158–160.

Semper C (1874) [1870–1885] Reisen im Archipel der Philippinen, Theil 2. Wissenschaftliche Resultate. Band 3, Landmollusken. Wiesbaden: Kreidel, 327 pp. [pp 129–168 (1874)]

Solem A (1966) Some non-marine mollusks from Thailand. Spolia Zoologia Musei Hauniensis 24: 1–110.

Sutcharit C, Pholyotha A (2023) Hidden lineages in the mountains: The genus *Glyptaulax* Gude, 1914 and *Maelamaodiscus* gen. nov. (Heterobranchia: Stylommatophora: Charopidae and Ariophantidae) with description of two new species from western Thailand. Tropical Natural History (Supplement 7): 123–138.

Sutcharit C, Jeratthitikul E, Pholyotha A, Lin A, Panha S (2020a) Molecular phylogeny reveals high diversity and endemism in the limestone karst-restricted land snail genus *Sophina* Benson, 1859 from Myanmar (Eupulmonata: Helicarionidae), with description of four new species. Journal of Zoological Systematics and Evolutionary Research 58(4): 957–981. https://doi.org/10.1111/jzs.12420

Sutcharit C, Thach P, Chhuoy S, Ngor PB, Jeratthitikul E, Siriwut W, Panha S (2020b) Annotated checklist of the land snail fauna from southern Cambodia (Mollusca, Gastropoda). ZooKeys 948: 1–46. https://doi.org/10.3897/zookeys.948.51671

Swainson W (1840) A treatise on malacology; or the natural classification of shells and shell-fish. Longman, London, 419 pp. https://doi.org/10.5962/bhl.title.8027

Tenison-Woods JE (1888) Malaysian land and freshwater Mollusca. Proceedings of the Linnean Society of New South Wales 3: 1003–1095. https://doi.org/10.5962/bhl.title.13026

Theobald W (1870) Descriptions of some new land shells from the Shan States and Pegu. Journal of the Asiatic Society of Bengal 39(1): 395–402.

Theobald W (1878) Notes on the land and freshwater shells of Kashmir, more particularly of the Jhilum valley below Srinagar and the hills north of Jammu. Journal of the Asiatic Society of Bengal 47(2): 141–149.

Theobald W, Stoliczka F (1872) Notes on Barmese and Arakanese land shells, with descriptions of a few new species. Journal of the Asiatic Society of Bengal 41(2): 329–334.

Thiele J (1931) [1929–1935] Handbuch der systematischen Weichtierkunde. Jena, Gustav Fischer, 1154 pp. [Volume 1, pp 1–376 (1929), pp 377–778 (1931), pp 779–1022 (1934); Volume 2, pp 779–1022 (1935)]

Tongkerd P, Lwin N, Páll-Gergely B, Chanabun R, Pholyotha A, Prasankok P, Seesamut T, Siriwut W, Srisonchai R, Sutcharit C, Panha S (2024) Contributions of a small collection of terrestrial microsnails (Pupilloidea, Hypselostomatidae) from Myanmar with description of three new species. ZooKeys 1195: 157–197. https://doi.org/10.3897/zookeys.1195.112112

van Benthem Jutting WSS (1952) Systematic studies on the non-marine Mollusca of the Ind-Australian archipelago. Treubia 21: 291–435.

van Benthem Jutting WSS (1959) Catalogue of the non-marine Mollusca of Sumatra and of its satellite islands. Beaufortia 7: 41–191.

Vaught KC (1989) A Classification of the Living Mollusca. American Malacologists, Inc., Melbourne, FL, 195 pp.

Vermeulen JJ, Liew TS, Schilthuizen M (2015) Additions to the knowledge of the land snails of Sabah (Malaysia, Borneo), including 48 new species. ZooKeys 531: 1–139. https://doi.org/10.3897/zookeys.531.6097

von Martens E (1860) On the Mollusca of Siam. Proceedings of the Zoological Society of London 28: 6–18. https://www.biodiversitylibrary.org/page/12866504

von Martens E (1864) Diagnosen neuer Heliceen aus dem ostasiatischen Archipel. Monatsberichte der Königlichen Preussischen Akademien der Wissenschaften zu Berlin 1864: 523–529. https://www.biodiversitylibrary.org/page/35180469#page/541/

von Martens E (1895) Die gattung *Cylindrus* Fitz. Archiv für Naturgeschichte 61(1): 103–108. https://www.biodiversitylibrary.org/item/47791

von Möllendorff OF (1891) On the land and freshwater shells of Perak. Proceedings of the Zoological Society of London 59(3): 330–348. https://doi.org/10.1111/j.1096-3642.1891.tb01757.x

von Möllendorff OF (1894) On a collection of land-shells from the Samui Islands, Gulf of Siam. Proceedings of the Zoological Society of London 62: 146–156. https://biodiversitylibrary.org/page/35990426

von Möllendorff OF (1899) Neue arten aus Hinterindien. Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft 31: 165, 166. https://biodiversitylibrary.org/page/28228787

Wade CM, Mordan PB, Clarke B (2001) A phylogeny of the land snails (Gastropoda: Pulmonata). Proceedings. Biological Sciences 268(1465): 413–422. https://doi.org/10.1098/rspb.2000.1372

Wade CM, Mordan PB, Naggs F (2006) Evolutionary relationships among the pulmonate land snails and slugs (Pulmonata, Stylommatophora). Biological Journal of the Linnean Society 87(4): 593–610. https://doi.org/10.1111/j.1095-8312.2006.00596.x

Westerlund CA (1887) Fauna der in der paläarctischen Region, lebenden Binnenconchylien. III. Gen. *Buliminus*, *Sesteria*, *Pupa*, *Stenogyra* & *Cionella*. Lund, Hakan Ohlsson, 183 pp. https://doi.org/10.5962/bhl.title.10301

Yu T-T, Páll-Gergely B, Salvador RB (2023) Caenogastropoda and Stylommatophora (Gastropoda) from the mid-Miocene Zhangpu amber of East Asia. Palaeoworld (Amsterdam) 32(4): 721–728. https://doi.org/10.1016/j.palwor.2022.07.004

Zilch A (1959) Gastropoda, Euthyneura. In: Schindewolf OH (Ed) Handbuch der Paläozoologie, Band 6, Gastropoda. Gebrüder Borntraeger, Berlin, 201–400.

Zilch A (1973) Die Typen und Typoide des Natur-Museums Senckenberg, 51: Mollusca: Achatinacea (2): Ferrussaciidae, Subulinidae. Archiv für Molluskenkunde 103: 99–152.

ZooKeys 1208: 241–258 (2024)
DOI: 10.3897/zookeys.1208.127135

Research Article

Resolution of the *Aleiodes seriatus* (Herrich-Schäffer, 1838)-aggregate in the western Palaearctic (Hymenoptera, Braconidae, Rogadinae), with description of a new species

Cornelis van Achterberg[1], Mark R. Shaw[2], Jose Fernandez-Triana[3], Donald L. J. Quicke[4]

1 *Naturalis Biodiversity Center, Postbus 9517, 2300 RA Leiden, Netherlands*
2 *National Museums of Scotland, Chambers Street, Edinburgh EH1 1JF, UK*
3 *Canadian National Collection of Insects, 960 Carling Avenue, Ottawa, Ontario, K1A 0C6, Canada*
4 *Integrative Insect Ecology Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University, Phayathai Road, Pathumwan, BKK 10330, Thailand*
Corresponding author: Cornelis van Achterberg (kees@vanachterberg.org)

Abstract

Two European species are recognised and characterised within the traditional *Aleiodes seriatus* species concept, based initially on DNA barcoding but with supporting, although slight and sometimes unreliable, morphological differences. *Aleiodes pseudoseriatus* **sp. nov.** is described and a neotype is designated for *Rogas seriatus* Herrich-Schäffer, 1838. Specimens from the Russian Far East were also DNA barcoded and were found to belong to a new species distinct from the two European taxa. The two European species were found to use different lithosiine hosts.

Key words: *Aleiodes pseudoseriatus* sp. nov., *Aleiodes seriatus*, *Atolmis rubricollis*, *Eilema griseola*, molecular barcodes, morphology, taxonomy

Academic editor: Xue-xin Chen
Received: 8 May 2024
Accepted: 22 June 2024
Published: 30 July 2024

ZooBank: https://zoobank.org/7FAC4BCC-37E7-4A68-B2DA-8CBEA5A614CE

Citation: van Achterberg C, Shaw MR, Fernandez-Triana J, Quicke DLJ (2024) Resolution of the *Aleiodes seriatus* (Herrich-Schäffer, 1838)-aggregate in the western Palaearctic (Hymenoptera, Braconidae, Rogadinae), with description of a new species. ZooKeys 1208: 241–258. https://doi.org/10.3897/zookeys.1208.127135

Introduction

At the time of the first part of our revision of the western Palaearctic species of *Aleiodes* Wesmael, 1838 (van Achterberg and Shaw 2016) we had cytochrome *c* oxidase subunit 1 sequences (CO1; DNA barcodes) for enough European specimens to be confident that there were two different species hidden under the name *A. seriatus* (Herrich-Schäffer, 1838), but not enough to engage in a fruitful analysis. We therefore took the decision to treat *A. seriatus* as an aggregate, and gave minimal data and illustration of it. In the intervening years, however, we have been able to DNA barcode many more specimens from various European localities, and can now present the results of combining the molecular (CO1) dataset with morphological analysis of the barcoded specimens (all but one in the National Museums of Scotland, NMS; the exception (MRS819) is in the Natural History Museum, London (NHMUK)) and other material, especially in both NMS and the Naturalis Biodiversity Center, Leiden (RMNH), to give diagnoses and descriptions of the two cryptic species.

Materials and methods

Morphology

Morphological analysis of molecular barcoded specimens (35 females, 26 males and one unsexed prepupa) was undertaken over a two-day period, and the characters found were tested on a further 212 specimens (including 84 females) from a wide range of European countries immediately afterwards. Series from single localities at which only one species occurred were instrumental (for *A. seriatus*: long series from England, Cambridgeshire, Chippenham Fen in the period 1983–1985 (27♀, 9♂); Czech Republic, České Budéjovice, Černiš wetland in 2009 (13♀, 21♂); and France, Var, Callas from 2017 to 2023 (14♀, 19♂).For the proposed new species, *A. pseudoseriatus*, we examined a shorter series from Cumbria, England and several sites from Sweden in the period 2004–2017). The analysis was later extended to include material from RMNH. The countries of origin of the specimens used (which are mostly in NMS or RMNH except for the long series of *A. seriatus* from Černiš wetland in the Institute of Entomology, České Budéjovice, Czech Republic, IECB, and a smaller number of other specimens as indicated) is given in the species accounts below.

Morphological terminology follows van Achterberg (1988, 1993) and van Achterberg and Shaw (2016), including the abbreviations for wing venation. Measurements are taken as indicated by van Achterberg (1988): for the length and the width of a body part, the maximum length and width are taken, unless otherwise indicated. The length of the mesosoma is measured from the anterior border of the mesoscutum to the apex of the propodeum, and of tergite I from the posterior border of the adductor to the medio-posterior margin of the tergite.

Observations and descriptions were made under an Olympus SZX11 stereomicroscope. Photographic images were taken with a Canon 5Ds 50.6-megapixel camera combined with a Canon MP-E 65 mm f/2.8 1–5× Macro lens, Laowa Macro Twin flash KX-800 and an electronic WeMacro Z-stepper rail. The photos were stacked with Helicon Focus 7 software. Some photographs were taken with a Keyence (VHX-7000) digital microscope.

Depositories

BZL	Oberösterreichisches Landesmuseum, Biologiezentrum, Linz, Austria
IECB	Institute of Entomology, České Budéjovice, Czech Republic
MSC	M. Schwarz collection, Linz, Austria
MTMA	Hungarian Natural History Museum, Budapest, Hungary
NHMUK	Natural History Museum, London, England
NMS	National Museums of Scotland, Edinburgh, Scotland
RMNH	Naturalis Biodiversity Center, Leiden, Netherlands
ZSM	Zoologische Staatssammlung, Munich, Germany

Molecular and phylogenetic methods

Specimens were DNA barcoded at the Biodiversity Institute of Ontario, University of Guelph, using their standard methods (Hrcek et al. 2011), generating an approximately 650 base pair, 5’ region cytochrome *c* oxidase subunit 1 (COI). Sequence alignment was trivial as there were no indels.

Sequence data were partitioned according to the three codon positions, and a maximum likelihood (ML) tree was constructed using RAxML-NG (Kozlov et al. 2019), with the GTR+FC+4Gm+BU model applied to each partition, and a full bootstrap also performed. The most likely tree was visualised using FigTree version 1.4.4. (Rambaut 2018). Three species which collectively bracket *A. seriatus* in the best tree presented by van Achterberg et al. (2020) were included as outgroups. A haplotype network was generated for the *A. seriatus* aggregate sequences using the program PopART (Leigh and Bryant 2015).

Results

Molecular results

The maximum likelihood phylogeny obtained (Fig. 1) shows that the sequenced individuals of the *A. seriatus*-aggregate form three clusters, with those from *A. seriatus* s. str. and the two specimens from the Russian Far East showing no, or very little, intraspecific sequence variation, and those of *A. pseudoseriatus* sp. nov. forming two small clusters but with little separation between them. *Aleiodes seriatus* s. str. was strongly supported (98% bootstrap) as being separate from the combined clusters representing *A. pseudoseriatus* sp. nov. and two putative French members of this species, though the latter two only received 58% bootstrap support. Consideration of the haplotype network (Fig. 2) shows that *A. seriatus* s. str. and the main cluster of *A. pseudoseriatus* sp. nov. sequences differ by a minimum of 34 base pairs. The two French specimens labelled as *A. ?pseudoseriatus* differ from *A. pseudoseriatus* sp. nov. and *A. seriatus* by a minimum 10 and 30 base pairs, respectively.

Morphology and descriptive taxonomy

The characters found were sufficient to provide unequivocal identification – at least for females – of about 90% of individual specimens, and much more than that if series are available. Males are less easy to determine with certainty, but (even if not barcoded) can often be confidently associated with females from the same locality. However, we have found one locality (France: Côte-d’Or, Abbaye de la Bussière) where light-trapping produced a good series of both species with seemingly identical body markings (some of each subsequently barcoded) on the same night.

Diagnosis of the *Aleiodes seriatus* aggregate (cf. van Achterberg and Shaw 2016)

It should be noted that the species aggregate here defined applies to the typical species *A. seriatus* (Herrich-Schäffer) and its nearest cryptic relatives, and is not the same as the broader concept of the *A. seriatus* species-group as expressed by Marsh and Shaw (1998), Fortier and Shaw (1999), Townsend and Shaw (2009), Shimbori and Shaw (2014), and Shaw et al. (2020), which has been applied more broadly to a morphologically-defined large assemblage of New World *Aleiodes* species with a margin of flat setae along the inner apex of the hind tibia.

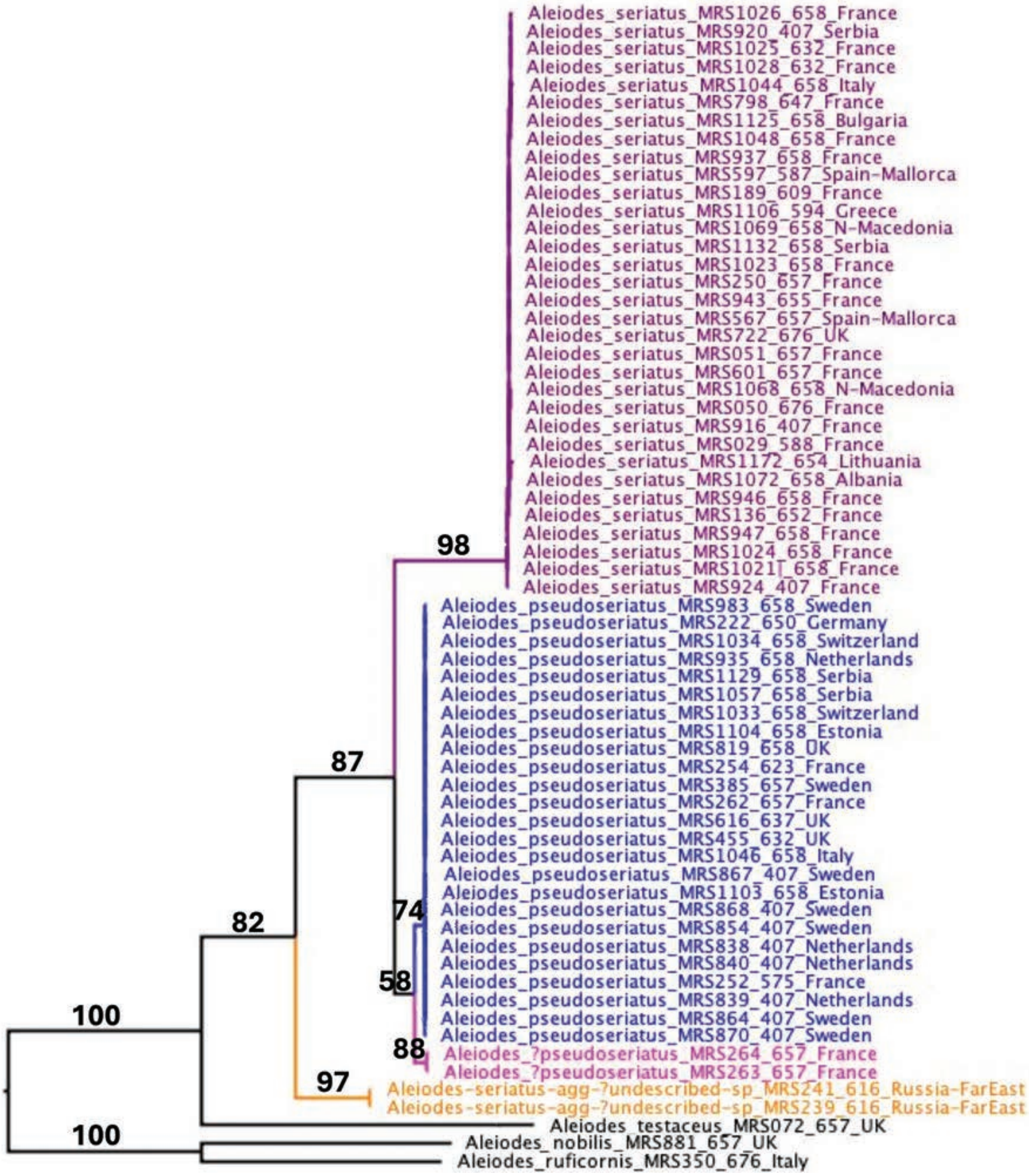


Figure 1. Maximum likelihood tree based on all DNA barcode sequence data for taxa included in this paper, rooted using sequences from three related *Aleiodes* species, with full bootstrap support values for selected branches.

Antennal segments of ♀ (35–)44–55, of ♂ (40–)46–58; length of malar space of ♀ 0.3–0.4× (of ♂ 0.25×) height of eye in lateral view (Figs 14, 18); OOL 0.8× diameter of posterior ocellus; temple narrow (Figs 13, 25); surroundings of veins 1-M and 1-SR of fore wing more or less infuscate (Figs 5, 19, 22, 23, 26, 28); inner apex of hind tibia with comb (Fig. 10); metasoma of ♀ maculate (Fig. 8) but in pale specimens less developed or absent (Figs 28, 29); fourth tergite of ♀ pale (ivory) yellowish latero-posteriorly, in ♂ usually infuscate or this tergite uniformly pale brown; base of hind tibia usually narrowly dark brown (Fig. 26); length of hind femur of ♀ 5.1–6.5× its width (of ♂ up to 8×); fourth tergite gently folded laterally, without acute lateral crease or this only anteriorly developed, although rarely present as a simple, non-lamelliform crease to apex of tergite; precoxal

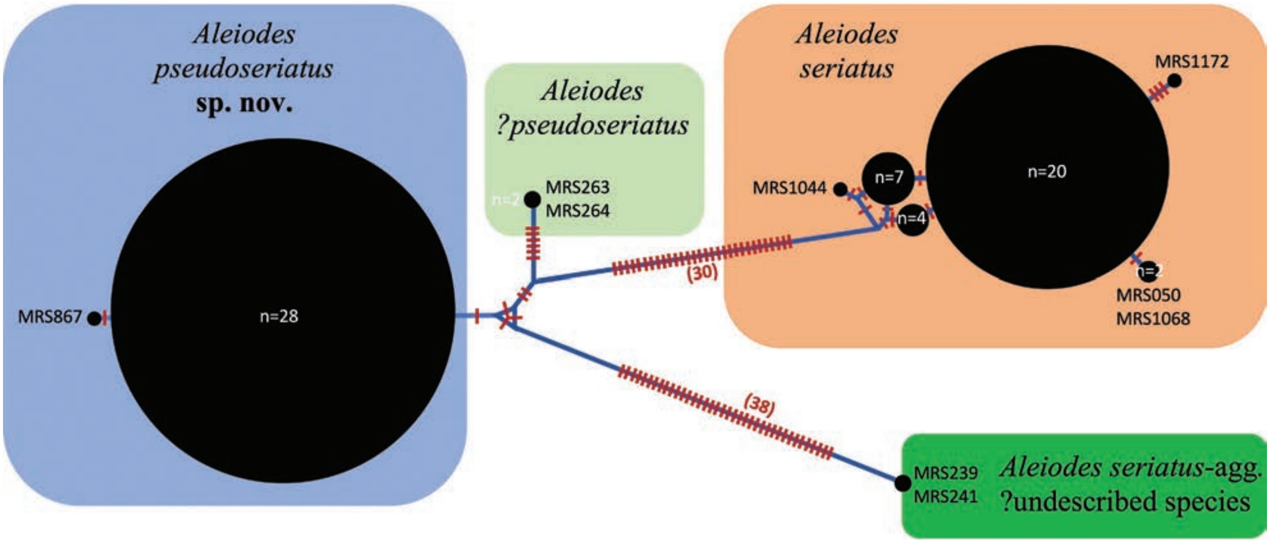


Figure 2. Median neighbour joining haplotype network for *A. seriatus* aggregate specimens.

area, epicnemial area and propodeum laterally, rugose; fourth tergite superficially transversely rugulose or aciculate; setose part of ovipositor sheath 0.6× as long as hind basitarsus. The patterning of the metasoma is characteristic but very variable in extent, and especially in pale specimens it may be absent (Figs 28, 29). Specimens with reddish and (almost) unmarked metasoma are rather frequent in southern populations of *A. seriatus*. Poorly marked forms (but almost never with completely pale metasoma) of *A. pseudoseriatus* sp. nov. seem less frequent and then have the second and third tergites more ivory than reddish.

Key to West Palaearctic species of the *A. seriatus* aggregate

1 Subbasal cell of fore wing setose apically (**aa** in Fig. 21); pterostigma distinctly pale yellowish antero-basally (Figs 22, 26, 28, 29)............................
***A. seriatus* (Herrich-Schäffer, 1838) [ca 80% of ♀, 50% of ♂, specimens]**

– Subbasal cell of fore wing with glabrous patch apically (**a** in Fig. 20); pterostigma variable, often with less developed pale yellowish patch or entirely brown antero-basally (Figs 3, 5)...**2**

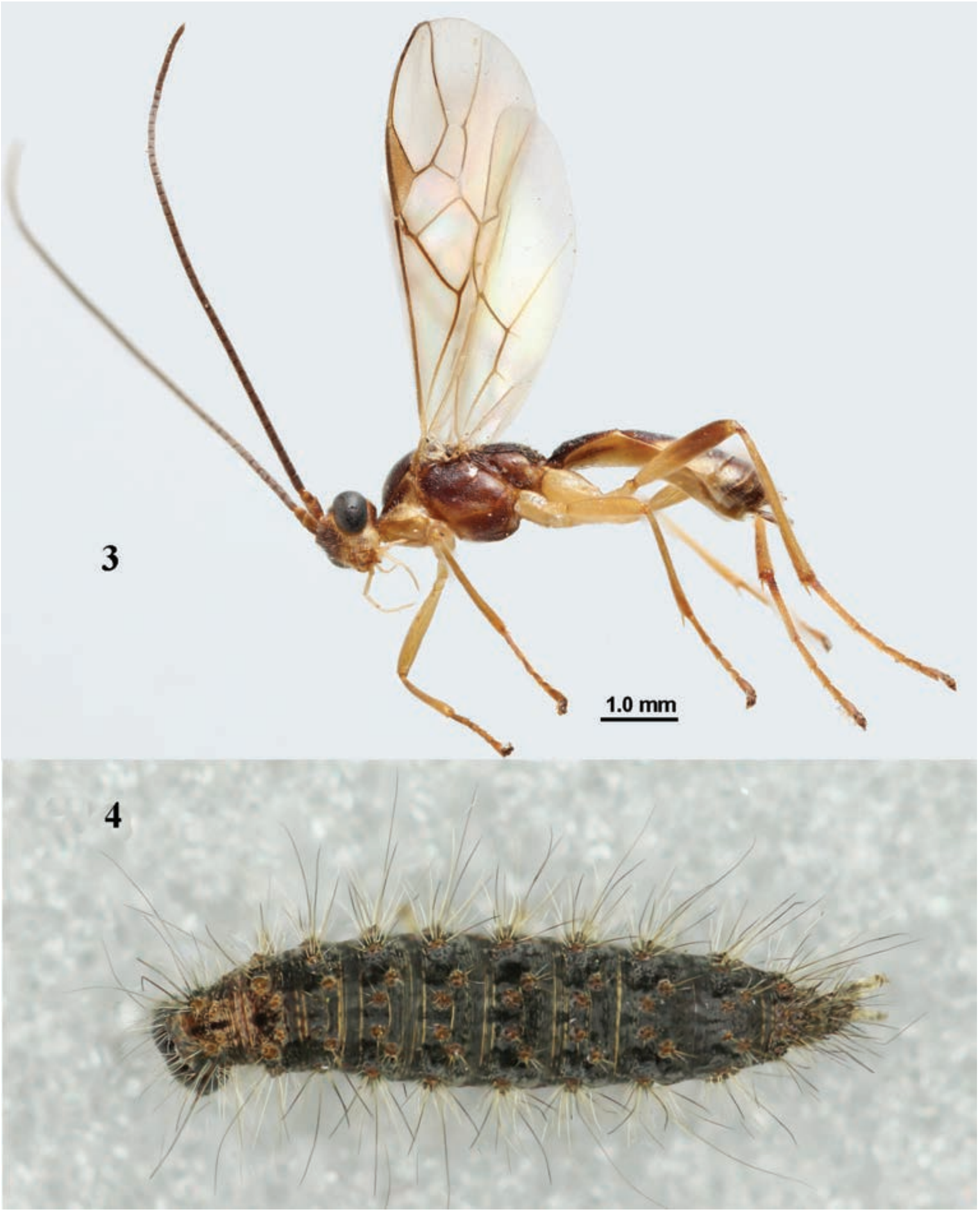
2 Glabrous patch in apical part of subbasal cell tending to be narrow and extending basad nearest to posterior margin (i.e., alongside 1-1A); pterostigma usually distinctly pale yellowish antero-basally (Figs 22, 26, 28); **if** (♀) hind femur partly dark brown laterally **then** also so ventrally; fourth antennal segment brown or yellowish brown ventrally, similar to scapus; vein 1-M of fore wing of ♂ and surrounding area often slightly less darkened ..
...***A. seriatus* (Herrich-Schäffer, 1838) [ca 20% of ♀, 50 of ♂, specimens]**

– Glabrous patch tending to be wider, when small or narrow more nearly equidistant between veins 1-CU1 and 1-1A (Fig. 20); pterostigma usually dark brown or brown antero-basally (Fig. 3), rarely yellowish in ♀ (but usually suffusedly so in ♂) (Figs 18, 19); **if** (♀) hind femur partly dark brown, **then** usually paler ventrally than laterally; fourth antennal segment dark brown (Figs 3, 15), **if** less brown **then** usually still darker than scapus ventrally (Fig. 18); vein 1-M of fore wing of ♂ and surrounding area often slightly more darkened (but variable in both species) .....***A. pseudoseriatus* sp. nov.**

Aleiodes pseudoseriatus van Achterberg & Shaw, sp. nov.

https://zoobank.org/C9AA7A50-C166-4CD1-94F8-E985995DE9EF
Figs 3–20

Type material. ***Holotype***, ♀ (NMS), "**Italy**, Veneto, Vittoria Veneto (VT), Frazione di fais, 46.017N 12.274E (WGS48), 450 m, 18.vii.2016, [at] UV light, D. Dal Pos", "MRS *Aleiodes* DNA 1064", "DNA COI worked". ***Paratypes***: 1 ♂ (BZL), **Austria**: Bad Ischl, OÖ [= Oberösterreich], Höherstein, 820 m, lux SW-wand, Forststrasse, N.47.686° E13.689°, 3.vii.2010, N. Pöll"; 1 ♂ (MSC), A[ustria]: Oberösterreich, 13 km SSW Reichraming, Krahlalm, 47°46'N, 14°23'E 22.vi.2011, 680–850 m, M. Schwarz"; 1 ♂ (BZL) "A-OÖ [= Austria: Oberösterreich], Linz-Urfahr, Pragerstrasse, N48.19.16 E14.17.36 18–19.vii.2013, Trefenthaler"; 1 ♂ (BZL), id., but "KGA Riesenhof, Parz 60 E14.16.15 N48.19.06, 5–8.ix.2013"; 1 ♂ (RMNH), "**Belgium**: Liège, Mt. Rigi, 650 m, 1–2.viii.1986, at light, C. Bank, RMNH"; 2 ♂ (RMNH), id., but 2.viii.1986, C. v. Achterberg; 1 ♀ (NMS), "**Bulgaria**: W Stara Planina Mts, confluence of Penkova and Berkovska rivers, 558 m, N43.2233 E023.07596, 10.ix.2021, S. Beshkov & A. Nahirnić-Beshkova"; 1 ♂ (BZL), "CZ [= **Czech Republic**]: Bohemia, C. Budéjovice, D. Voda, N48°58' E14°32' 470 m, M. Halada 10.vii.2001"; 1 ♀ (NMS), "[**England**:], Cumbria, Howe, Whitbarrow, [at] MV light, 24.viii.[19]95, M.R. Shaw"; 1 ♂ (NMS), "Cum[bria], Roudsea Wood, at light, 15.vii.[20]06, M.R. Shaw", "MRS *Aleiodes* DNA 455", "DNA CO1 worked"; 1 ♂ (NMS), id., but "MRS *Aleiodes* DNA 616", "DNA CO1 worked"; 1 ♂ (NHMUK), "England: E. Kent, West Wood, TR1426143868, MV light, 29.viii.2011", "MRS *Aleiodes* DNA 819", "DNA CO1 worked"; 1 ♀ (NHMUK), "England, Cornwall, Ding Dong, Tredinnick Stack, SW444348 MV light trap, J. Herbert, BMNH(E) 2012-41"; 1 ♂ (NHMUK), "[England]: Hen Wood, SU6522 Hants VC11, 23.vii.2013 MV"; 1 ♀ (NMS), "**Estonia**: Piargu, Raplamaa Farmland, [N]59.122167, [E]24.831745, 9.ix.2019 MV light, Kaido Kärner", "MRS *Aleiodes* DNA 1103", "DNA CO1 worked"; 1 ♂ (NMS), id., but "MRS *Aleiodes* DNA 1104", "DNA CO1 worked"; 1 ♀ (NMS), "**France**: Côte d'Or, Abbaye de la Bussière, La Bussière-sur-Ouche, at light, 19.vii.2003, M.R. Shaw", "MRS *Aleiodes* DNA 262", "DNA COI worked"; 1 ♀ (NMS), id., but "MRS *Aleiodes* DNA 254", "DNA CO1 worked"; 1 ♀ (NMS), id., but "MRS *Aleiodes* DNA 252", "DNA CO1 worked"; 1 ♂ (RMNH), "France: Finistère, Forêt du Cranou, 7 km E [of] le Faou, on *Taxus*, 27.vi.1988, M.J. Gijswijt"; 1 ♀ (RMNH), "France: Doubs, RN Lac de Remoray, 16.viii.2009, Mal. tr[ap] 3, 948242/6634536, H. Gens, RMNH'23"; 1 ♀ (NMS), "**Finland**: Oulu, Ketolanoja, Muhos, Mal.tr. 5–19. viii.[20]05, N. Laurenne"; 1 ♀ (NMS), "**Germany**: Bayerswald, 2001, M. Kuhlmann", "MRS *Aleiodes* DNA 222", "DNA CO1 worked"; 1 ♂ (RMNH), "Germany: Thüringen, NP Hainich, nr Eisenach, [reared] from *Fagus sylvatica* stems, 12.vi-3.vii.2008, M. Gossner, RMNH'08"; 1 ♀ (ZSM), "[Germany]: Ober Bayern, Garmisch, 12–1300 m, 10.viii.1936, E. Bauer"; 2 ♀ (ZSM), "[Germany]: Ebenhausen, Isart, viii.[19]40, K.V. Rosen"; 7 ♂ (MTMA), "**Hungary**, Nógrád m., Bátonyterenye (Kisterenye), Csente, Kertvárosi kert", "48.0074992°/19.8180737° [= 20.viii–9.ix.2016], P.G. Sulyán, lámpázás (6)"; 1 ♂ (MTMA), id., but "[= 24.ix–30.ix. 2016]... lámpázás (8)"; 1 ♂ (MTMA), id., but [= 15.x.2016]...lámpázás (9)"; 1 ♀ (NMS), "[**Ireland**]: Wexford, 5.vii.[19]02, J.J.F.X. King"; 1 ♀ (NHMUK), "[Ireland]: Kilkea Deerpark, Co, W[e]x[-ford], 4.vi.1937, A.W. Stelfox"; 3 ♀ + 2 ♂ (NMS), "**Italy**: Veneto, Riserva Naturale Integrale Bosco Nordio, Chioggia, 45.122N 12.260E, 28.vii.2016, D. Dal Pos"; 2 ♂ (NMS), id., but "3.vi.2016"; 1 ♂ (NMS), "**Netherlands**: Noord Holland duinreservaat, Egmond aan Zee, MV 8.vii.2016, M.R. Shaw", "MRS *Aleiodes* DNA 838", "DNA CO1 worked”; 1 ♂ (NMS), id., but “MRS *Aleiodes* DNA 839”, “DNA CO1 worked”; 1 ♂ (NMS), id., but “MRS *Aleiodes* DNA 840”, “DNA CO1 worked”; 2 ♂ (NMS), id., but no DNA labels1 ♂ + 1 ♀ (RMNH), “Netherlands: Gld, Tongeren, 3.ix.1991, B. v. Aartsen”; 1 ♀ (RMNH), id., but 9.vii.1989, C.J. Zwakhals; 1 ♀ (RMNH), “Netherlands: LI, Brunssum-Treebeek, c. 100 m, 50°56'17"N, 5°56'58"E, garden, at light, 25–31.vii.2018, G. Lommen, RMNH”; 1 ♂ (RMNH), id., but 3–10.vi.2018; 1 ♀ (RMNH), “[Netherlands: UT,] 3bergen [= Driebergen], Six [c. 1860]”; 1 ♀ (RMNH), “[? Netherlands, Hilvarenbeek], H.B., 3.vii”; 1 ♂ (RMNH), “Nederland: Gld, ‘t Harde, 16.viii.1993, B. v. Aartsen”; 1 ♀ (RMNH), “Netherlands[: FR], Fochtelo, 4.ix.2001, B. v. Aartsen; 1 ♀ (RMNH), “Netherlands: DR, Borger, Boswachterij Borger, UTM LD, 495693, SBB-vak 26, 25–28.vii.1993, Mal. tr[ap], L. Witmond”; 1 ♀ (RMNH), “Netherlands: NB, Tilburg, Kaaistoep, at light, 18.vii.2017, 128.8–394.6, T. Peeters, RMNH’18”; 1 ♀ (RMNH), “[Netherlands:] Gld, Epe, de Dellen, 19.vii.1994, B. v. Aartsen”; 1 ♂ (RMNH), “[Netherlands:] OV, Hasselt, Stadsgaten, 24.vii.1994, B. v. Aartsen”; 3 ♀ (RMNH), “Netherlands: NB, Achtmaal, O. Bluisse Heide, MT, R.D. 97–386, 5.viii.2015, E. Brosens”; 1 ♂ (RMNH), id., but 15.viii.2015; 1 ♀ (NMS), “**Norway**: RY Hølland, 58.52445N 5.83518E, 17.vii–2.vii.2020 Mal. tr. A.T. Mjøs”; 1 ♂ (NMS), “**Serbia**: Kasan, N of Prepollent, 1256 m, 43°19'35"N, 19°96'44"E, 3.vii.2019, C.W. Plant”, “MRS *Aleiodes* DNA 1057”, “DNA COI worked”; 1 ♀ (NMS), “Serbia: Tzaribrod (Dimitrovgrad) distr., Vištni Kamen above Bačevo Village, 763 m, N43.0271, E022.8239 11.viii.2021, S. Beshkov & A. Nahirnić-Beshkova”, “MRS *Aleiodes* DNA 1129”, “DNA CO1 worked”; 1 ♀ + 3 ♂ (NMS), “Serbia: Suva Planina, Preslap, 1186 m, N43.19473 E022.24400, 30.vi.2021, S. Beshkov & A. Nahirnić-Beshkova”; 1 ♀ (NHMUK), “Yugoslavia, **Slovenia**, Postojne, 24.vii, R.L. Coe”; 1 ♀ (RMNH), “Espana [= **Spain**:] Huesca, Torla, 1035 m, 8–26.vii.1974, J. Wolschrijn”; 1 ♀ (NMS), “**Sweden**: Bohuslän, Tossene, Åby, MV, 9.vii–13.viii.2013, N. Ryrholm”, “MRS *Aleiodes* DNA 864”, “DNA CO1 worked”; 1 ♂ (NMS), id., but “14.viii–21.xi.2013” and no DNA labels; 1 ♂ (NMS), “Sweden: Bohuslän, Tossene, Stora Hultet MV, 8.viii–21.xi.2013 N. Ryrholm, “MRS *Aleiodes* DNA 867”, “DNA CO1 worked”; 1 ♂ (NMS), id., but “MRS *Aleiodes* DNA 868”, “DNA CO1 worked”; 1 ♂ (NMS), id, but “28.v–5.viii.2013” and no DNA labels; 1 ♂ (NMS), “Sweden: Gästrikland, Staffen, Grinduga, MV, 23.vii–9.9.2013 N. Ryrholm”, “MRS *Aleiodes* DNA 870”, “DNA CO1 worked”; 1 ♂ (NMS), “Sweden: Ha[lland],Ysby Perstorp, 1–8.viii.2004, N. Ryrholm, NMSZ 2004.167”, “MRS *Aleiodes* DNA 385”, “DNA CO1 worked”; 2 ♂ (NMS), id., but no DNA labels; 1 ♂ (NMS), “Sweden: Skåne, Ö Hoby, Spraggehusen, MV, 1.ix–30.x.2013 N. Ryrholm”, “MRS *Aleiodes* DNA 854”, “DNA CO1 worked”; 2 ♂ (NMS), id., but no DNA labels: 1 ♂ (NMS), “Sweden: Skåne, Spraggehusen, MV, 20.v–16.vii.2017 N. Ryrholm/C. Källender”, “MRS *Aleiodes* DNA 983”, “DNA CO1 worked”; 2 ♀ + 4 ♂ (NMS), “Sweden: Skåne, Käseberga, Käseberga,17.vii–14.ix.2013, N. Ryrholm”; 1 ♀ (NHMUK), “Sweden: Sk[åne], Degaberga, 8.vii.1938, D.M.S. P[erkins] & J.F. P[erkins], B.M. 1938-414”; 1 ♀ + 1 ♂ (NHMUK), id., but “10.vii.1038”; 1 ♀ (NHMUK), id., but “14.vii.1938”; 3 ♀ (NHMUK), “Sweden: Skåne, Löderup, 27.vii.1938, D.M.S. P[erkins] & J.F. P[erkins], B.M. 1938-414” 1 ♀ (NMS), **Switzerland**: BE, Lenk, Brandegg, 1540 m, 29.vi–3.vii.2019, M.R. Shaw”, “MRS *Aleiodes* DNA 1033”, “DNA CO1 worked”; 1 ♀ (NMS), id., but “MRS *Aleiodes* DNA 1034”, “DNA CO1 worked”; 1 ♀ (NHMUK), “Switzerland: Grindelwald, viii.1937, G. Nixon”;1 ♀ (RMNH), “CH [= Switzerland]: Lauerz, SZ, Schuttwald, 480 m, 8.viii.1990, Lf, L. Rezbanyai-Reser”; 1 ♂ (RMNH), id., but 26.vi.1990; 1 ♂ (RMNH), id., but 11.ix.1991; 1 ♂ (RMNH), id., but Sägel (Ried), 455 m, 24.vii.1990. Most unassociated males are considered too doubtfully determined to be treated as paratypes.



Figures 3, 4. *Aleiodes pseudoseriatus* sp. nov., paratype, ♀ (**3**), and mummified caterpillar of *Atolmis rubricollis* (Linnaeus) with *A. pseudoseriatus* larva within (**4**), both from England, S. Cumbria, Whitbarrow. **3** habitus, lateral view **4** mummy, dorsal view.

Molecular data. We have DNA barcoded material from England, Estonia, France, Germany, Italy, Netherlands, Serbia, Sweden and Switzerland (see Fig. 1).

Biology. The record (Fahringer 1934) of *A.* "*vittiger*" from *Atolmis* (as *Gnophria*) *rubricollis* (Linnaeus) (Lepidoptera: Erebidae, Arctiinae, Lithosiini) is presumed to relate to this species, but we have not seen a reared specimen ourselves except for one partially formed adult extracted from a mummy of this host from Austria that is, unfortunately, not in good enough condition to be determined unequivocally as *A. pseudoseriatus*. However, we have barcoded the dead parasitoid prepupa (MRS935) from a failed mummy of this moth from the Netherlands and it clusters in the tree unequivocally with *A. pseudoseriatus*. Also, at a site in S. Cumbria, England where *A. pseudoseriatus* is the only one of the two relevant *Aleiodes* we have found (and barcoded), we have on several occasions obtained mummies of *A. rubricollis* that must undoubtedly have harboured *A. pseudoseriatus*, though unfortunately, none survived to produce adults of the parasitoid. The host is increasingly widely distributed and abundant in Europe, and its larva feeds on algae on (often dead) twigs of trees, perhaps with a special liking for conifers, from about July into October. It overwinters as a pupa (unlike *Eilema griseola*), so in this case the parasitoid overwinters in the host mummy and has proved to be difficult to rear. To judge from their behaviour in captivity, parasitised *Atolmis rubricollis* larvae probably descend from trees to mummify in the litter rather than the mummy forming on twigs. *Aleiodes pseudoseriatus* is univoltine with a flight time from the very end of June to September.

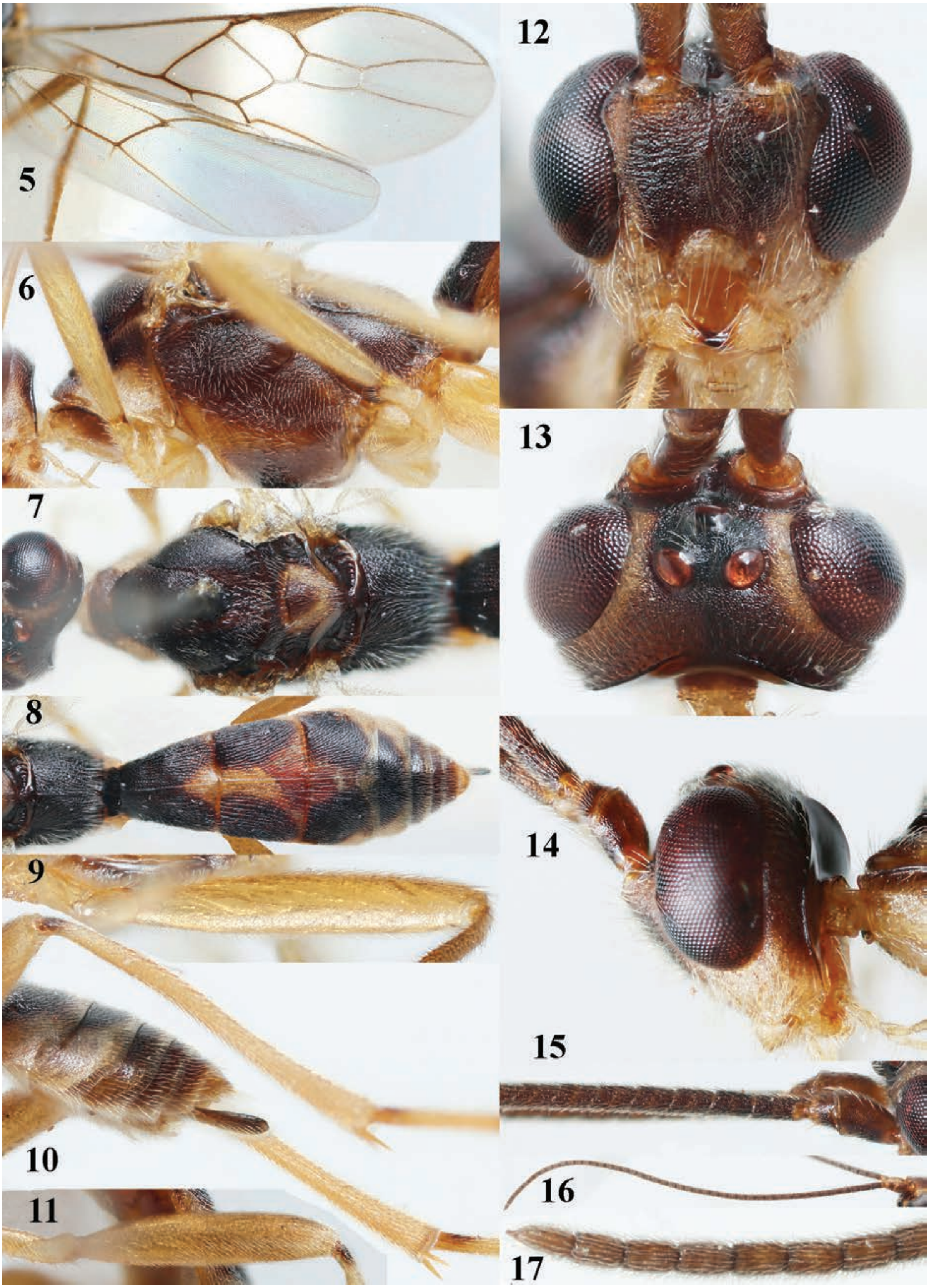
A female paratype (not barcoded but confidently determined and from the area in England (S. Cumbria) where only *A. pseudoseriatus* has been found (and barcoded)), was offered cultured larvae of the lithosiin arctiine *Eilema griseola* (Hübner) at various stages of growth in viii.1995, by day and at dusk when she was more active, but apart from very brief antennation on a minority of occasions she showed no interest in them.

Diagnosis. Subbasal cell of fore wing with small glabrous patch apically (**a** in Fig. 20); pterostigma variable, often with less-developed pale yellowish patch or entirely brown antero-basally (Figs 3, 5); hind femur of ♀ usually 4.7–5.5× longer than wide; pterostigma usually dark brown or brown antero-basally, rarely yellowish (Figs 5, 18, 19); **if** ♀ hind femur partly dark brown, then usually paler ventrally than laterally; fourth antennal segment dark brown (Figs 3, 15), if brown then darker than scapus ventrally (Fig. 18); vein 1-M of fore wing of ♂ and surrounding area often darker than in *A. seriatus*. On average with about 3 more antennal segments than *A. seriatus* in both sexes. We have also seen the holotype of *Rogas kuslitzkyi* Tobias, 1976, from Azerbaijan and believe it can be ruled out to belong to *A. pseudoseriatus* (see also notes on barcoded specimens from Primorsky Krai below).

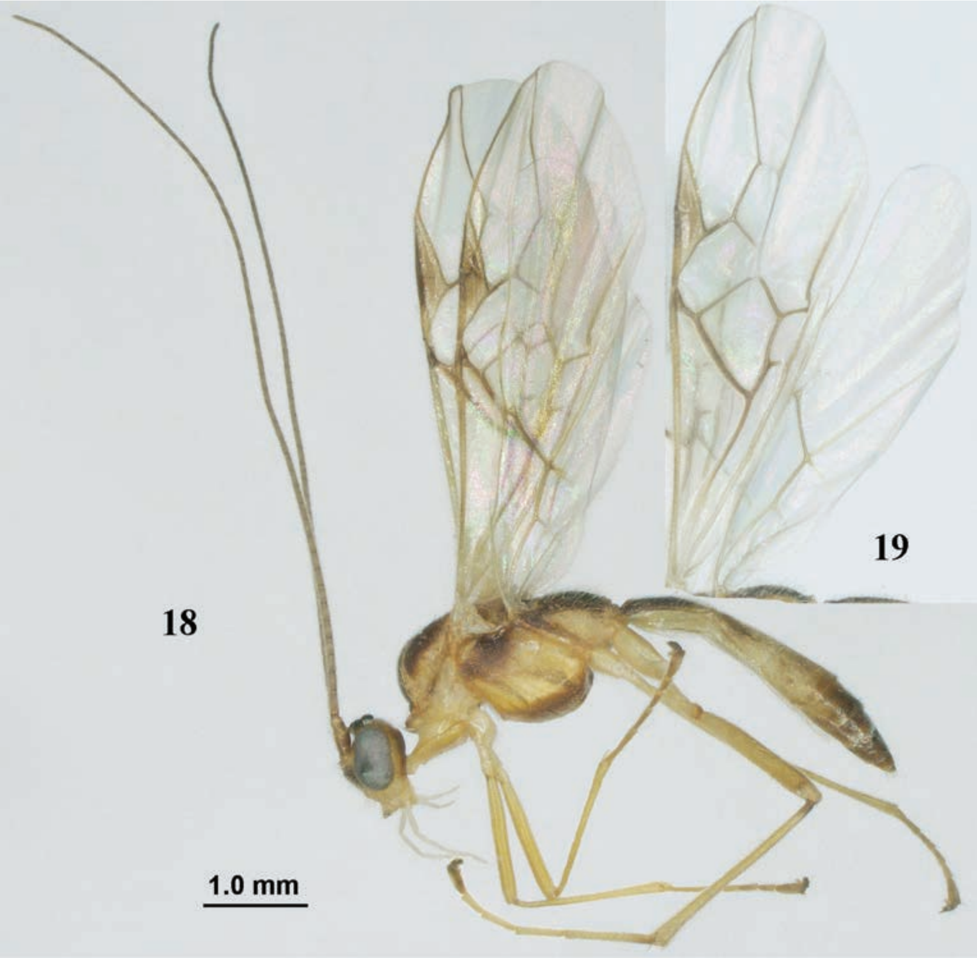
Description. Holotype, ♀, length of fore wing 5.2 mm, of body 5.9 mm.

***Head*.** Antenna incomplete, but according to label originally with 47 segments, length of antenna in ♀ paratype from England 1.3× fore wing and its subapical segments medium-sized (Fig. 17); frons granulate and distinctly depressed laterally; OOL 1.5× diameter of posterior ocellus, granulate and matt; depression near posterior ocellus granulate; vertex largely granulate-coriaceous, rather dull; clypeus coriaceous; ventral margin of clypeus depressed (Fig. 12); face granulate but dorsally rugulose; width of hypoclypeal depression 0.4× minimum width of face (Fig. 12); length of eye 3.6× temple in dorsal view (Fig. 13); vertex behind stemmaticum rugulose-granulate; clypeus largely above lower level of eyes; length of malar space 0.3× length of eye in lateral view.

***Mesosoma*.** Mesoscutal lobes finely granulate-coriaceous, matt; precoxal area of mesopleuron rugulose but posteriorly absent, and area above it finely granulate; metapleuron densely granulate and ventrally rugose; metanotum with short median carina anteriorly and distinct depression posteriorly; scutellum finely granulate; propodeum rather long and flat, granulate anteriorly and densely rugose posteriorly, medio-longitudinal carina complete, and without protruding carinae laterally.



Figures 5–17. *Aleiodes pseudoseriatus* sp. nov., holotype, ♀, Italy, Vittoria Veneto, but 17 of paratype ♀ from England, Whitbarrow. **5** wings **6** mesosoma, lateral view **7** mesosoma, dorsal view **8** propodeum and metasoma, dorsal view **9** fore femur, lateral view **10** ovipositor sheath **11** hind femur, lateral view **12** head anterior **13** head, dorsal view **14** head, lateral view **15** base of antenna **16** antenna **17** apex of antenna.



Figures 18–19. *Aleiodes pseudoseriatus* sp. nov., paratype, ♂, England, S. Cumbria, Roudsea Wood. **18** habitus, lateral view **19** wings.

Wings. Fore wing: r 0.4 × 3-SR (Fig. 5); 1-CU1 horizontal, 0.7 × 2-CU1; r-m 0.3 × 3-SR; second submarginal cell medium-sized (Fig. 5); cu-a inclivous, straight; 1-M straight posteriorly; 1-SR as wide as 1-M; surroundings of M+CU1, 1-M and 1-CU1 setose, but subbasal cell with small glabrous patch apically (a in Fig. 20). Hind wing: marginal cell parallel-sided, its apical width 1.1× width at level of hamuli (Fig. 5); 2-SC+R as long as wide; short m-cu present anteriorly; vein 2-1A absent (Fig. 5); M+CU:1-M: 1r-m = 30:18:18.

Legs. Tarsal claws rather robust, bristly setose and very finely yellowish pectinate; hind coxa rather shiny and only very superficially micro-sculptured, dorsally granulate; hind trochantellus rather slender (Fig. 11); length of hind femur and basitarsus 5.1 and 8.3× their width, respectively; length of inner hind spur 0.2× hind basitarsus; apex of hind tibia with distinct comb at inner side (Fig. 10).

Metasoma. First tergite distinctly convex medially, as long as wide apically; first and second tergites with medio-longitudinal carina, weakly indicated on third tergite; first tergite densely longitudinally rugose; second and third tergites more or less obliquely rugulose (Fig. 8); medio-basal area of second tergite triangular and minute (Fig. 8); second suture deep and distinctly crenulate; remainder of metasoma superficially micro-sculptured or smooth; fourth and apical half of third tergite without sharp lateral crease; ovipositor sheath widened, with medium-sized slanted setae and apically subtruncate (Fig. 10).

***Colour*.** Dark brown; palpi, legs (but base of hind tibia dark brown), mandible (except dark brown teeth), malar space, clypeus and tegulae pale yellowish; orbita, propleuron, side of pronotum, mesosternum anteriorly, scutellum largely, first tergite medio-apically, second tergite medially (area widened posteriorly) and third tergite antero-medially yellowish brown; antenna, veins and pterostigma (but slightly paler basally than medially) mainly dark brown; third-sixth tergites posteriorly and laterally ivory (Figs 3, 8); wing membrane subhyaline, but surroundings of veins 1-M, 1-SR, 1-CU1 and r of fore wing more or less infuscate (Figs 5, 18).

Distribution (from type material involved in this study): Austria, Belgium, Bulgaria, Czech Republic, England, Estonia, France, Finland, Germany, Hungary, Ireland, Italy, Netherlands, Norway, Serbia, Slovenia, Spain, Sweden, Switzerland.

Etymology. The species is named *"pseudoseriatus"*, because of its similarity to *A. seriatus*.

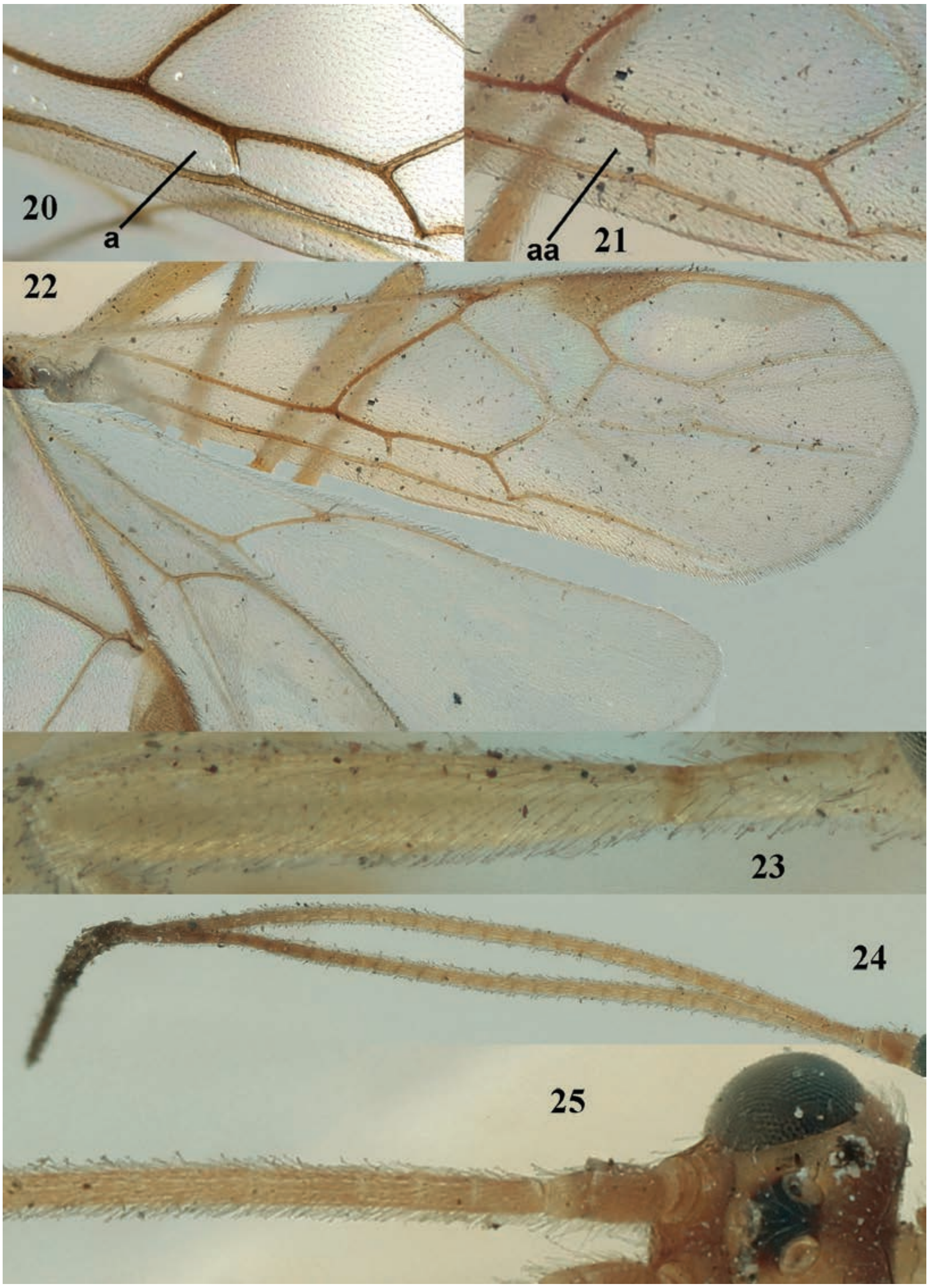
Variation. Pterostigma colour is rather variable, often with indistinct pale yellowish patch or entirely brown antero-basally, but sometimes with distinct yellowish basal patch; hind femur of ♀ usually 4.7–5.5 times longer than wide; ♀ with 46(1), 47(3), 48(8), 49(15), 50(13), 51(1) antennal segments and ♂ with 48(1), 50(2), 51(5), 52(14), 53(14), 54(11), 55(5), 56(4), 58(1) antennal segments; fourth antennal segment dark brown (Fig. 15), if brown then darker than scapus ventrally, rarely both are yellow; hind femur entirely yellowish brown or with faint brown small patch to large dark brownish part; metasoma with typical black pattern. Specimens with almost unmarked metasoma seem to occur very rarely or possibly not at all. Males have, on average, about three or four more antennal segments than females.

Aleiodes seriatus **(Herrich-Schäffer, 1838)**

Figs 21–29 (see also figs 328–340 in van Achterberg and Shaw (2016))

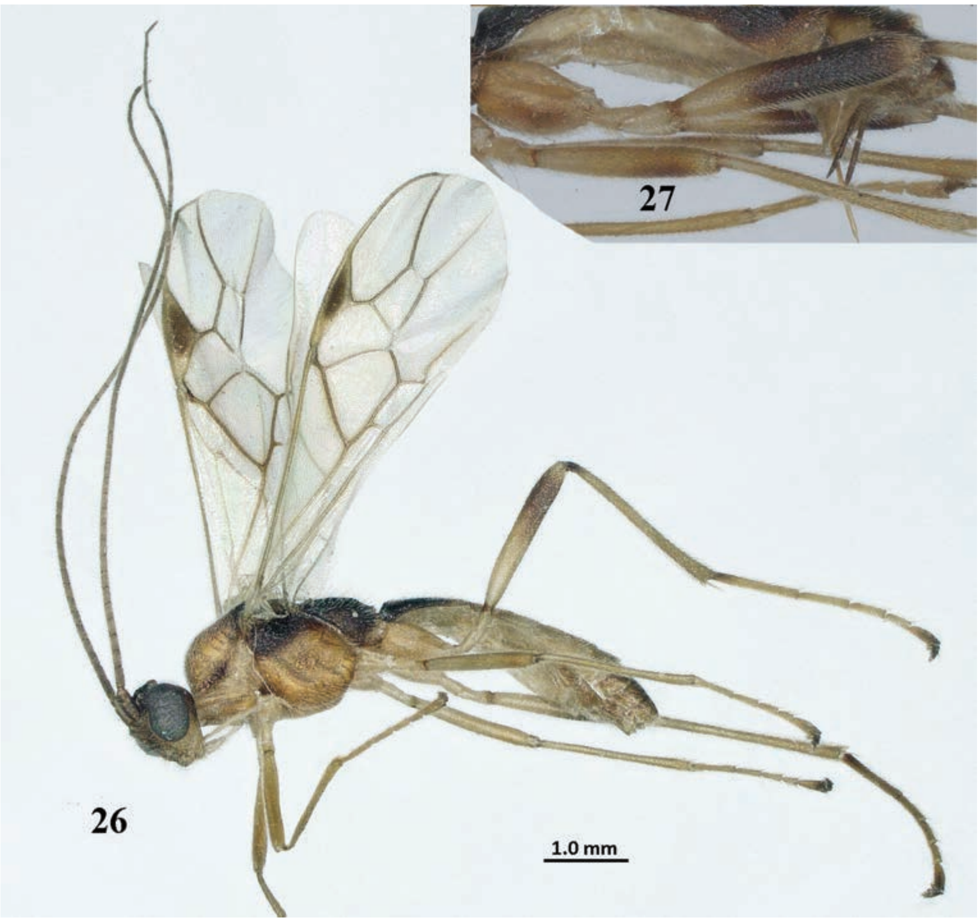
Rogas seriatus Herrich-Schäffer, 1838: 156–12, fig. [type series lost].
Aleiodes seriatus; Papp 1991: 107; Belokobylskij et al. 2003: 399.
Aleiodes vittiger Wesmael, 1838: 112; Shenefelt 1975: 1185; Papp 1991: 107; Belokobylskij et al. 2003: 399 (as synonym of *A. seriatus*) [examined].
Rogas kuslitzkyi Tobias, 1976: 88, 223–224; 1986: 83 (1995 transl.: 137).
Aleiodes kuslitzkyi; Belokobylskij et al. 2003: 399 (as synonym of *A. seriatus*).

Type material. The type series of *Aleiodes seriatus* (Herrich-Schäffer) is lost; as are the types of other Braconidae described by Herrich-Schäffer (Horn and Kahle 1935–1937; CvA could not find any specimen in the Zoological Museum in Berlin). The original description is rudimentary, and the figure shows only the colour pattern (which is highly variable) and there is a cryptic species in Europe. Considering the description (distinct yellowish base of the pterostigma), origin of the type series (assumed to be collected in the surroundings of Regensburg, Bavaria (his residence)) and its similarity with the lectotype of *A. vittiger*, this lectotype (♀, Royal Belgian Institute of Natural Sciences, Brussels, "*A. vittiger*, ♀, mihi, 13" (in Wesmael's handwriting), "*A. vittiger* mihi, dét. C. Wesmael", "Coll. Wesmael", "Belgique, Bruxelles", "Lectotypus ♀ *Aleiodes vittiger* Wesm., 1838, Papp, 1983") is herewith designated as the neotype of *A. seriatus* (Herrich-Schäffer, 1838) to stabilize the taxonomy of the nominal species *A. seriatus* and *A. vittiger*.



Figures 20–25. *Aleiodes seriatus* aggregate: holotype of *A. pseudoseriatus* sp. nov. (**20**), *Aleiodes seriatus* (Herrich-Schäffer), lectotype of *A. vittiger* Wesmael, ♀, Belgium (**21–25**) **20, 21** detail of distal half of subbasal cell of fore wing ("a" indicating comparatively large glabrous patch and "aa" a minute glabrous patch) **22** wings **23** fore femur **24** antennae **25** base of antenna. Photographs by Julian Lalanne except 20.

Molecular data. We have barcoded specimens from Albania (Gjurokaster), Bulgaria (Godech), England (Cambridgeshire), France (Ardèche, Corsica, Côte-d'Or, Dordogne, Var), Greece (Meteora), Italy (Veneto), Lithuania (Cepheliai), North Macedonia (Vardar), Serbia (Dukat, Suva Planina) and Spain (Mallorca: S'Albufera) (see Figs 1, 2).



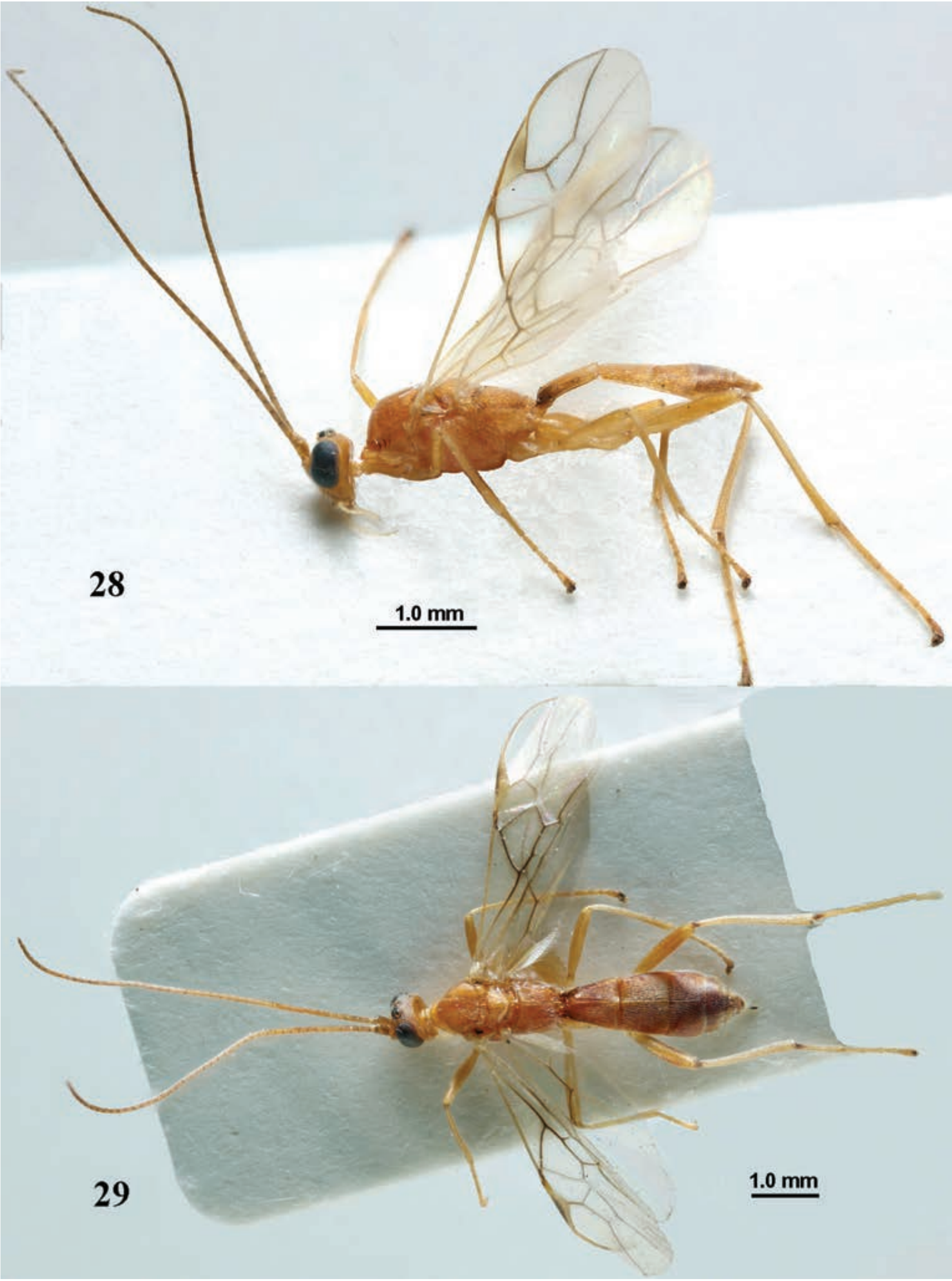
Figures 26, 27. *Aleiodes seriatus* (Herrich-Schäffer), ♂ (**26**) and ♀ (**27**), England, Chippenham Fen. **26** habitus, lateral view **27** detail of hind femur and ovipositor sheath.

Additional material. Austria, Czech Republic, Netherlands (DR: Borger, Wijster, LI: St. Pietersberg, NB: Tilburg (Kaaistoep), Oisterwijk), Germany, Hungary, Montenegro, Poland, Russia, Sweden, Turkey.

Diagnosis. Subbasal cell of fore wing setose apically (aa in Fig. 21; in ca 80% of ♀ specimens, 50% of ♂); pterostigma often distinctly pale yellowish antero-basally (Figs 22, 28, 29); hind femur of ♀ 5.3–6.0 times longer than wide (in ♂ up to 7.2 times); **if** (♀) hind femur partly dark brown laterally then also so ventrally; fourth antennal segment brown or yellowish brown ventrally, similar to scapus (Fig. 28); vein 1-M of fore wing of ♂ and surrounding area often less darkened than in *A. pseudoseriatus*.

Variation. Antenna of ♀ with 44(2), 45(10), 46(16), 47(20), 48(16), 49(5), 50(2), 51(1) antennal segments and of ♂ 46(2), 47(5), 48(8), 49(19), 50(16), 51(10), 52(4), 53(6), 54(2),55(4) segments. Males have, on average, about three or four more antennal segments than females.

Biology. The only reared specimen seen is a male, accompanied by the host mummy, labelled as from *Lithosia griseola* (= *Eilema griseola* (Hübner), Lepidoptera: Erebidae, Arctiinae, Lithosiini) with the date 23/6.[19]33 from Hatert (Netherlands), in the E. Bauer collection (ZSM). The mummy is compatible, but it is unclear whether the date recorded is of collection or emergence, though probably the latter – but the rearing might nevertheless have been artificially advanced indoors. The host overwinters as a small larva, and presumably the



Figures 28, 29. *Aleiodes seriatus* (Herrich-Schäffer) pale form, ♂ (**28**) and ♀ (**29**), France, Taradeau. **28** habitus lateral **29** habitus dorsal.

parasitoid does so as an early instar larva inside the living host. It is notable that this increasingly widespread moth is found especially in wet woodland, fen carr, etc., and we have seen a long series of *A. seriatus* trapped in such places: Chippenham Fen, England (in NMS), and Černiš wetland, near České Budějovice, Czech Republic (in IECB). We have also seen a female specimen (in E. Bauer collection, ZSM) reared in 1927 in the Netherlands labelled as coming from *Malacosoma neustria* (= *Malacosoma neustria* Linnaeus, Lepidoptera: Lasiocampidae) but there is no mummy present and we discount this as a credible record, not least on the grounds that this moth has a conspicuous and commonly reared caterpillar from which there are no further recorded rearings of

A. seriatus (which, at least as an aggregate, is a distinctive entity likely to have been recorded). While capture dates mostly suggest a flight period of June to August into September, we have seen five specimens (including four males) collected in October – as well as a further eight males taken in September. These late males rather strongly suggest that there may be a (perhaps only partial) second generation, raising the possibility that a succession of *Eilema* species, with differing phenology, might constitute the host repertoire overall.

Distribution (from material involved in this study): Albania, Austria, Bulgaria, Czech Republic, England, France (including Corsica), Germany, Greece, Hungary, Italy, Lithuania, Montenegro, Netherlands, North Macedonia, Poland, Russia, Serbia, Spain (Mallorca), Sweden and Turkey.

Discussion

In common with most Lithosiini, the known hosts of the two *Aleiodes* species treated here are both becoming increasingly widespread and abundant in Europe, perhaps due to the recent change in atmospheric pollutants from a burden of sulphur dioxide, highly deleterious for algae, to increased levels of nitrogen oxides which encourage algal growth on aerial twigs. Probably the two *Aleiodes* species will prove to co-occur in an increasing number of localities.

In the tree, there are two sequences, MRS263 and MRS264, of female specimens that are morphologically indistinguishable from *A. pseudoseriatus* but cluster separately from it. While we acknowledge that there may be several reasons for this, they were collected at a site in France, Côte-d'Or, alongside specimens of both *A. seriatus* and *A. pseudoseriatus* (both barcoded) and, because we have found that other close *Aleiodes* species do sometimes hybridize in culture and produce female offspring (in prep.), we consider it possible that they are hybrids, albeit of unknown fitness.

Rogas kuslitzkyi Tobias, 1976 was synonymized with *A. seriatus* by Belokobylskij et al. (2003). At first, we believed that the sequences MRS239 and MRS241 of specimens from Primorsky Krai in the Russian Far East might belong to *A. kuslitzkyi*, which we have not been able to distinguish reliably from *A. pseudoseriatus* or *A. seriatus*. However, *A. kuslitzkyi* was described from the Caucasus region which is much closer to Europe than to the Far East of Russia. Considering the region and the colour of the pterostigma, it seems most likely that *A. kuslitzkyi* is indeed a synonym of *A. seriatus* as published by Belokobylskij et al. (2003) and that the Far East Russian (together with NW Chinese specimens we have seen elsewhere) belong to another new species. The number of antennal segments of both female types of *A. kuslitzkyi* (45, 47) also fits in with *A. seriatus* and excludes *A. pseudoseriatus*.

Acknowledgements

Thanks to Berdien Daniels, Wouter Dekoninck and Julian Lalanne (Royal Belgian Institute of Natural Sciences, Brussels) for supplying photographs of the lectotype of *Aleiodes vittiger*, Sergey Belokobylskij (Zoological Institute, St. Petersburg) for information about the type of *A. kuslitzkyi* and Aleš Bezděk (IECB) for a large loan of *A. seriatus*. DLJQ was supported by the Rachadaphisek Somphot Fund for postdoctoral fellowship, Graduate School, Chulalongkorn

University. Funding for DNA barcoding was provided by Agriculture and Agri-Food Canada Project J-002276 “Systematics of beneficial arthropods in support of resilient agroecosystems”. Both reviewers (Sergey Belokobylskij and Scott Shaw) are gratefully acknowledged for their helpful contributions.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

No funding was reported.

Author contributions

All authors have contributed equally.

Author ORCIDs

Cornelis van Achterberg https://orcid.org/0000-0002-6495-4853
Mark R. Shaw https://orcid.org/0000-0002-6651-8801
Jose Fernandez-Triana https://orcid.org/0000-0003-0425-0309

Data availability

All of the data that support the findings of this study are available in the main text.

References

Belokobylskij SA, Taeger A, van Achterberg C, Haeselbarth E, Riedel M (2003) Checklist of the Braconidae (Hymenoptera) of Germany. Beiträge zur Entomologie 53(2): 341–435. https://doi.org/10.21248/contrib.entomol.53.2.341-435

Fahringer J (1934) *Opuscula braconologica* III. Palaearktische Region II. Wagner, Wien.

Fortier JC, Shaw SR (1999) Cladistics of the *Aleiodes* lineage of the subfamily Rogadinae (Hymenoptera: Braconidae). Journal of Hymenoptera Research 8(2): 204–237.

Herrich-Schäffer GAW (1838) Faunae Insectorum Germaniae initiae oder Deutschlands Insecten. Hymenoptera. Heft 156. Regensburg.

Horn W, Kahle I (1935–1937) Über entomologische Sammlungen, Entomologen & Entomo- Museologie, ein Beitrag zur Geschichte der Entomologie. Entomologische Beihefte aus Berlin-Dahlem 2–4: i–vi, 1–536.

Hrcek J, Miller SE, Quicke DLJ, Smith MA (2011) Molecular detection of trophic links in a complex insect host-parasitoid food web. Molecular Ecology Resources 11(5): 786–794. https://doi.org/10.1111/j.1755-0998.2011.03016.x

Kozlov AM, Darriba D, Flouri T, Morel B, Stamatakis A (2019) RAxML-NG: A fast, scalable, and user-friendly tool for maximum likelihood phylogenetic inference. Bioinformatics (Oxford, England) 35(21): 4453–4455. https://doi.org/10.1093/bioinformatics/btz305

Leigh JW, Bryant D (2015) POPART: Full-feature software for haplotype network construction. Methods in Ecology and Evolution 6(9): 1110–1116. https://doi.org/10.1111/2041-210X.12410

Marsh PM, Shaw SR (1998) Revision of North American *Aleiodes* (part 3): the *seriatus* species-group (Hymenoptera: Braconidae: Rogadinae). Proceedings of the Entomological Society of Washington 100(3): 395–408.

Papp J (1991) Second survey of the braconid wasps in the Bátorliget Nature Conservation Areas, Hungary (Hymenoptera: Braconidae). Studia Naturalia 1(2) (1990): 639–674. In: The Bátorliget Nature Reserves after forty years. Magyar Természettudományi Múzeum, Budapest.

Rambaut A (2018) Figtree 1.4.4. Institute of Evolutionary Biology, University of Edinburgh, Edinburgh.

Shaw SR, Shimbori EM, Penteado-Dias A (2020) A revision of the *Aleiodes bakeri* (Brues) species subgroup of the *A. seriatus* species group with the descriptions of 18 new species from the Neotropical Region (Hymenoptera: Braconidae: Rogadinae). ZooKeys 964: 41–107. https://doi.org/10.3897/zookeys.964.56131

Shenefelt RD (1975) Braconidae 8. Exothecinae, Rogadinae. Hymenopterorum Catalogus (nova editio). Pars 12: 1115–1262.

Shimbori EM, Shaw SR (2014) Twenty-four new species of *Aleiodes* Wesmael from the eastern Andes of Ecuador with associated biological information (Hymenoptera, Braconidae, Rogadinae). ZooKeys 7402: 1–81. https://doi.org/10.3897/zookeys.405.7402

Tobias VI (1976) Opredelitel Faune SSSR 110: 1–286. [Braconids of the Caucasus (Hymenoptera, Braconidae)] [in Russian]

Townsend A, Shaw SR (2009) Nine new species of *Aleiodes* reared from caterpillars in the northeastern Andes of Ecuador (Hymenoptera: Braconidae: Rogadinae). Journal of Insect Science 9(33): 1–21. https://doi.org/10.1673/031.009.3701

van Achterberg C (1988) Revision of the subfamily Blacinae Foerster (Hymenoptera, Braconidae). Zoologische Verhandelingen Leiden 249: 1–324.

van Achterberg C (1993) Illustrated key to the subfamilies of the Braconidae (Hymenoptera: Ichneumonoidea). Zoologische Verhandelingen Leiden 283: 1–189.

van Achterberg C, Shaw MR (2016) Revision of the western Palaearctic species of *Aleiodes* Wesmael (Hymenoptera, Braconidae, Rogadinae). Part 1: Introduction, key to species groups, outlying distinctive species, and revisionary notes on some further species. ZooKeys 639: 1–164. https://doi.org/10.3897/zookeys.639.10893

van Achterberg C, Shaw MR, Quicke DLJ (2020) Revision of the western Palaearctic species of *Aleiodes* Wesmael (Hymenoptera, Braconidae, Rogadinae). Part 2: Revision of the *A. apicalis* group. ZooKeys 919: 1–259. https://doi.org/10.3897/zookeys.919.39642

Wesmael C (1838) Monographie des Braconides de Belgique 4. Nouveaux Mémoires de l'Academie Royale des Sciences et Belles-lettres de Bruxelles 11: 1–166. https://doi.org/10.3406/marb.1837.2702

ZooKeys 1208: 259–274 (2024)
DOI: 10.3897/zookeys.1208.124047

Research Article

Two new species of the genus *Halichoanolaimus* (Nematoda, Selachinematidae) from the intertidal zone of the Yellow Sea, China

Mian Huang[1], Hongxiu Zhai[1]

1 *College of Life Sciences, Liaocheng University, Liaocheng 252059, China*
Corresponding author: Mian Huang (huangmian@lcu.edu.cn)

Abstract

Two new marine nematode species belonging to the genus *Halichoanolaimus* from the intertidal zone of the Yellow Sea are described. *Halichoanolaimus sinensis* **sp. nov.** is characterized by amphideal fovea with 2.5–3.0 turns, 20–27% of corresponding body diameters; spicules curved, middle portion broad, tapering distally, 1.4–1.5 cloacal body diameters long; gubernaculum slender consisting of two detached lateral pieces tapering distally; 10–13 papilliform precloacal supplements in two groups, the posterior three supplements smaller and closer to each other, the remaining supplements larger and widely spaced; tail conico-cylindrical with a half cylindrical portion. The second new species, *Halichoanolaimus zhangi* **sp. nov.** is distinct by having lateral differentiation present except in anterior half of pharynx which has even punctations, amphideal fovea with 3.0–3.3 turns, spicules curved, gradually narrowing from proximal to distal end with pointed tip, 7 papilliform precloacal supplements, gradually increasing the spacing distance forward, two rows of subventral conical setae situated at the precloacal region, tail elongated, filiform. An updated key to 30 valid species of *Halichoanolaimus* is provided.

Key words: Biodiversity, free-living marine nematode, *Halichoanolaimus sinensis* sp. nov., *Halichoanolaimus zhangi* sp. nov., identification key, taxonomy

Academic editor: Alexei Tchesunov
Received: 27 March 2024
Accepted: 29 June 2024
Published: 31 July 2024

ZooBank: https://zoobank.org/CA37DEF5-365F-4B12-AC70-78C5E7EEA7BE

Citation: Huang M, Zhai H (2024) Two new species of the genus *Halichoanolaimus* (Nematoda, Selachinematidae) from the intertidal zone of the Yellow Sea, China. ZooKeys 1208: 259–274. https://doi.org/10.3897/zookeys.1208.124047

Introduction

The Yellow Sea is located on the edge of the western Pacific Ocean, between the Chinese mainland and the Korean Peninsula. It is a semi-enclosed inland shallow sea basin. Biodiversity surveys and taxonomical studies on nematodes in the Yellow Sea have been carried out in recent years. More than 350 species of nematodes have been identified, of which 105 species were new to science (Hao et al. 2022; Chu et al. 2023). The new species accounted for 30% of the known species. However, the total number of nematodes in this sea area is unknown, and new species are routinely found. It is, therefore, important to continue investigating the taxonomy of nematodes in the region.

The genus *Halichoanolaimus* was established by de Man (1886) with the type species of *H. robustus* (Bastian, 1865). It is a common and diverse genus of predatory nematodes belonging to the family Selachinematidae and found from shallow seas to the abyssal plain (Miljutin et al. 2010; Leduc 2020).

The most recent species descriptions were provided by Xiao and Guo (2023). Based on the reviews by Tchesunov (2014), Leduc and Zhao (2016), Leduc (2020) and Huang and Guo (2022), *Halichoanolaimus* is characterized by a cuticle with lateral differentiation in the form of larger and more widely spaced punctations; all anterior sensilla papilliform; a buccal cavity consisting of two parts separated by a row of teeth; pharynx without bulb; precloacal supplements usually papilliform or setiform and tail conico-cylindrical, elongated with a distal filiform portion, or conical. Within *Halichoanolaimus*, the species are distinguished by rather few main characters: the number of amphidial turns, number and arrangement of precloacal supplements, structure of spicules and gubernaculum, and shape and length of the tail. A key to the identification of 22 valid species for the genus was given by Zograf et al. (2015). Subsequently, six species, *H. anisospermus* Leduc & Zhao, 2016, *H. stagnalis* Gagarin & Long, 2017, *H. funestus* Leduc, 2020, *H. ossilagulus* Leduc, 2020, *H. pumilus* Leduc, 2020 and *H. sicaoensis* Xiao & Guo, 2023, were described. To date, 28 valid species within *Halichoanolaimus* have been recorded worldwide.

Materials and methods

In order to investigate the diversity of free-living nematodes along the coast of the Yellow Sea, China, sediment samples were collected in several intertidal sites in 2008 and 2022 respectively. The meiofauna samples were obtained from the top sediment layer (0–8 cm deep) using a 2.9 cm diameter sawn-off syringe. The samples were fixed with an equal amount of 10% formalin solution.

In the laboratory, samples were stained with 0.1% Rose Bengal for more than 12 hours (Higgins and Thiel 1988). The stained samples were poured into two layers of sieves (500 and 30 μm mesh sizes) respectively, and washed with tap water to remove silt and separate macrofauna from meiofauna. The heavier sediment particles retained on the 30-micrometer mesh were removed using centrifugation with Ludox-TM colloidal silica (50% colloidal silica suspension in water; Sigma Aldrich Co., USA) with a specific gravity of 1.15 g/ml (de Jonge and Bouwman 1977). Each sample was washed into a Petri dish with distilled water and meiofauna was sorted under a stereoscopic microscope (Olympus SZ 51). Nematodes were transferred into a 9:1 (v/v) solution of 50% alcohol-glycerol in an embryo dish to slowly evaporate to pure glycerol, and then mounted into permanent slides (McIntyre and Warwick 1984).

Finally, the specimens were mounted in glycerin on permanent slides. Observation and measurement were carried out using a differential interference contrast microscope (Leica DM 2500) and Leica software of LAS X version 3.3.3. Line drawings were made with the aid of a camera lucida. Type specimens were deposited in the Marine Biological Museum of the Chinese Academy of Sciences, Qingdao.

Abbreviations are as follows: **a**, the ratio of body length to maximum body diameter; **abd**, body diameter at cloaca or anus; **b**, ratio of body length to pharynx length; **c**, ratio of body length to tail length; **cbd**, corresponding body diameter; **c'**, ratio of tail length to cloacal or anus body diameter; **V%**, position of vulva from anterior end expressed as a percentage of total body length.

Results and discussion

Taxonomy

Class Chromadorea Inglis, 1983
Order Chromadorida Chitwood, 1933
Family Selachinematidae Cobb, 1915

Genus *Halichoanolaimus* De Man, 1886

Diagnosis (modified from Leduc 2020). Cuticle with lateral differentiation in the form of larger and more widely spaced punctations. All anterior sensilla usually papilliform. Buccal cavity separated into two chambers by transversal sets of denticles; posterior chamber of buccal cavity surrounded by three Y-shaped pairs of cuticularized rhabdions. Pharynx without anterior or posterior bulb. Intestine of adult stages blind. Precloacal supplements usually papilliform or setiform. Tail with conical proximal portion and often elongated cylindrical distal portion.

Valid species list

Halichoanolaimus anisospermus Leduc & Zhao, 2016
Halichoanolaimus balochiensis Turpeenniemi, Nasira & Maqbool, 2001
Halichoanolaimus bispirae Daschenko & Belogurov, 1991
Halichoanolaimus brandtae Zograf, Trebukhova & Pavlyuk, 2015
Halichoanolaimus caucasicus Sergeeva, 1973
Halichoanolaimus chordiurus Gerlach, 1955
Halichoanolaimus consimilis Allgén, 1933
Halichoanolaimus dolichurus Ssaweljev, 1912
Halichoanolaimus duodecimpapillatus Timm, 1954
Halichoanolaimus funestus Leduc, 2020
Halichoanolaimus lanceolatus Vitiello, 1970
Halichoanolaimus lukjanovae Sergeeva, 1973
Halichoanolaimus macrophallus Gourbault & Vincx, 1985
Halichoanolaimus macrospiculatus Hopper, 1961
Halichoanolaimus minor Ssaweljev, 1912
Halichoanolaimus minutissimus Timm, 1961
Halichoanolaimus norvegicus Allgén, 1940
Halichoanolaimus ossilagulus Leduc, 2020
Halichoanolaimus ovalis Ditlevsen, 1921
Halichoanolaimus possjetiensis Belogurov & Fadeeva, 1980
Halichoanolaimus pumilus Leduc, 2020
Halichoanolaimus quattuordecimpapillatus Chitwood, 1951
Halichoanolaimus raritanensis Hasbrouck, 1966
Halichoanolaimus robustus (Bastian, 1865) de Man, 1886
Halichoanolaimus sicaoensis Xiao & Guo, 2023
Halichoanolaimus sonorus Belogurov & Fadeeva, 1980
Halichoanolaimus stagnalis Gagarin & Long, 2017
Halichoanolaimus unicus Inglis, 1968

***Halichoanolaimus sinensis* sp. nov.**

https://zoobank.org/3BCBB4D2-AED6-4A98-81B5-F637EA95290F

Figs 1, 2, Table 1

Material examined. Four males and two females were obtained. ***Holotype***: ♂1 on slide RZ08-7-5; ***paratypes***: ♂2 on slide RZ08-7-2, ♂3 on slide RZ08-7-5, ♂4 and ♀1 on slide RZ08-7-3, and ♀2 on slide RZ08-7-2. Type specimens were deposited in the Marine Biological Museum of the Chinese Academy of Sciences, Qingdao.

Type locality and habitat. Holotype and all additional specimens were found from intertidal silt sediment at Rizhao coast of the Yellow Sea; 35°26'N, 119°34'E; 0–2 cm and 2–5 cm sediment depth.

Etymology. The specific epithet refers to the country origin, China.

Measurements. All measurement data are given in Table 1.

Description. Males. Body cylindrical, tapering slightly towards posterior end. Cuticle with transverse rows of punctations, lateral differentiation consisting of slightly larger and more widely spaced punctations. Cuticle pore not observed. Somatic setae short, 3 μm long, sparsely distributed. Lip region slightly rounded. Six inner labial sensilla papillose; six outer labial sensilla setiform, 3–4 μm long, at same level as four papilliform cephalic sensilla (Fig. 2C). Amphideal fovea multispiral with 3 turns (Fig. 2B), 25–27% of corresponding body diameter in width, located at the level of the middle of buccal cavity, ca 20 μm from anterior end of body. Buccal cavity large, ca 45 μm deep, divided into anterior and posterior portions by two rows of 15–17 denticles. Anterior portion of buccal cavity cup-shaped, with three sets of three cuticularized rhabdions; posterior portion of buccal cavity narrower, cylindrical, surrounded by three Y-shaped pairs of cuticularized rhabdions with swollen bases, 20 μm long. Pharynx cylindrical, anterior end swelling, wrapped the buccal cavity, without posterior bulb. Pharyngeal lumen cuticularized. Nerve ring at ca 44% of pharynx length from anterior end. Secretory-excretory system present. Renette cell small, situated at level of cardia; ampulla large, excretory pore situated slightly posterior to the nerve ring, ca 180 μm from the anterior end. Cardia small, surrounded by intestine.

Reproductive system diorchic with two opposed, outstretched testes. Anterior testis to the right or ventrally to intestine, posterior testis to the left side of intestine. Spicules paired, curved, middle portion broad, tapering distally, 1.4–1.5 cloacal body diameters long, interior of spicules granular in appearance. Gubernaculum slender, consisting of two detached lateral pieces tapering distally, adjoining the dorsal side of spicules. 10–13 papilliform precloacal supplements in two groups, the posterior three supplements smaller and closer to each other (Fig. 2E), located 7 μm from the cloaca; 5 μm from each other; remaining supplements larger and widely spaced, ca 25 μm from each other. Each supplement consisting of conical papilla and an internal duct. Tail conico-cylindrical with posterior cylindrical portion comprising about half of total tail length. Caudal setae absent. Three caudal glands located posterior to spicules, spinneret present, 7 μm long.

Females. Similar to males, but with slightly larger body and slightly smaller amphideal fovea (20% of corresponding body diameter in width and with 2.5 turns). Reproductive system didelphic, with two opposed, reflexed ovaries. Anterior ovary to the left of intestine and posterior ovary to the right of intestine. Vulva situated slightly pre-median. Intestine blind, anus not observed.

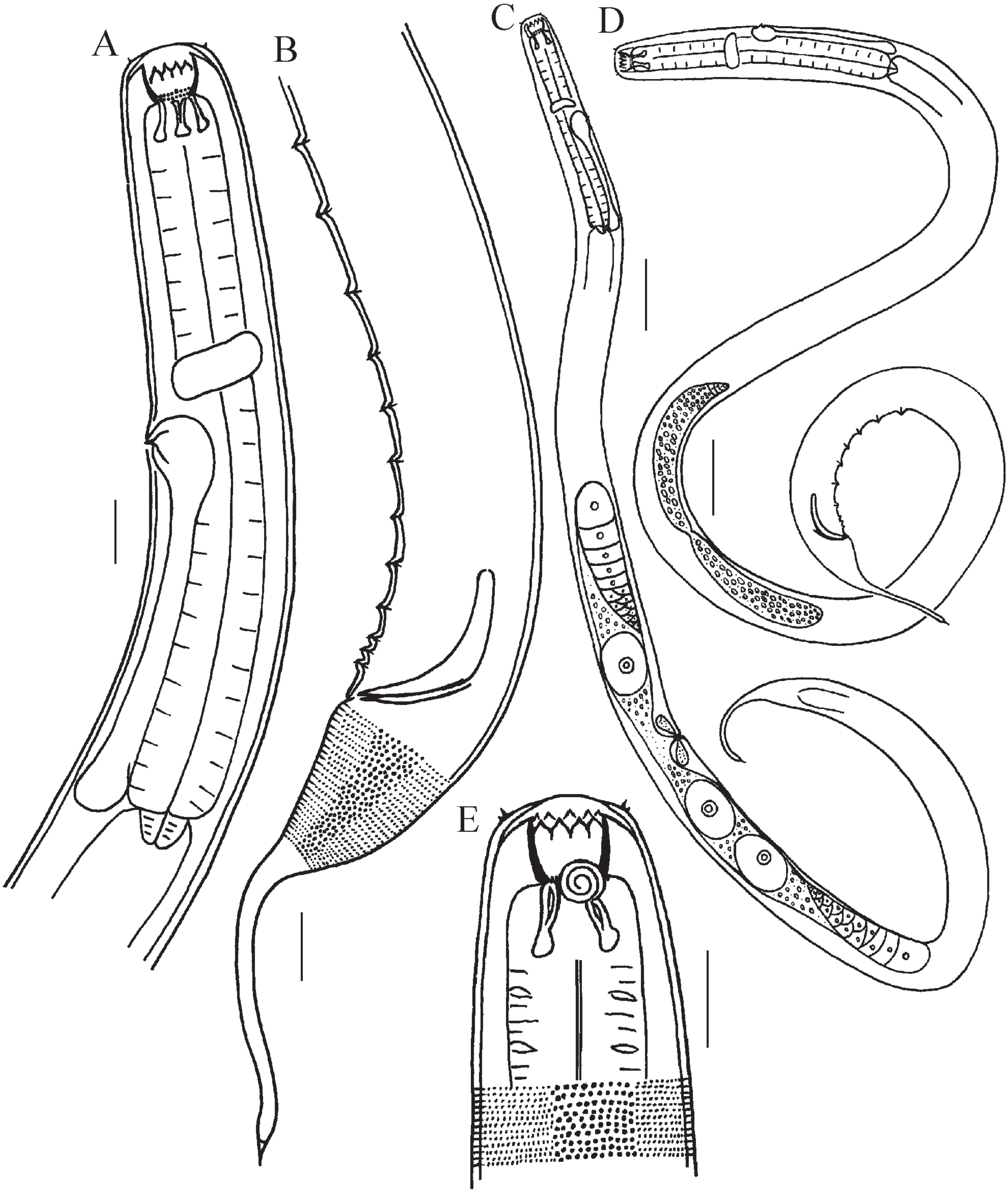


Figure 1. Drawings of *Halichoanolaimus sinensis* sp. nov. **A** pharyngeal region of male **B** posterior end of male **C** entire body of female **D** entire body of male **E** anterior end of male. Scale bars: 30 μm (**A, B, E**); 100 μm (**C, D**).

Differential diagnosis and discussion. *Halichoanolaimus sinensis* sp. nov. is characterized by amphideal fovea with 2.5–3.0 turns, 20–27% of corresponding body diameter; spicules curved, middle portion broad, tapering distally, 1.4–1.5 cloacal body diameters long; gubernaculum slender consisting of two detached lateral pieces tapering distally; 10–13 papilliform precloacal supplements in two groups, the posterior three supplements smaller and closer to each other, remaining supplements larger and widely spaced; tail conico-cylindrical with

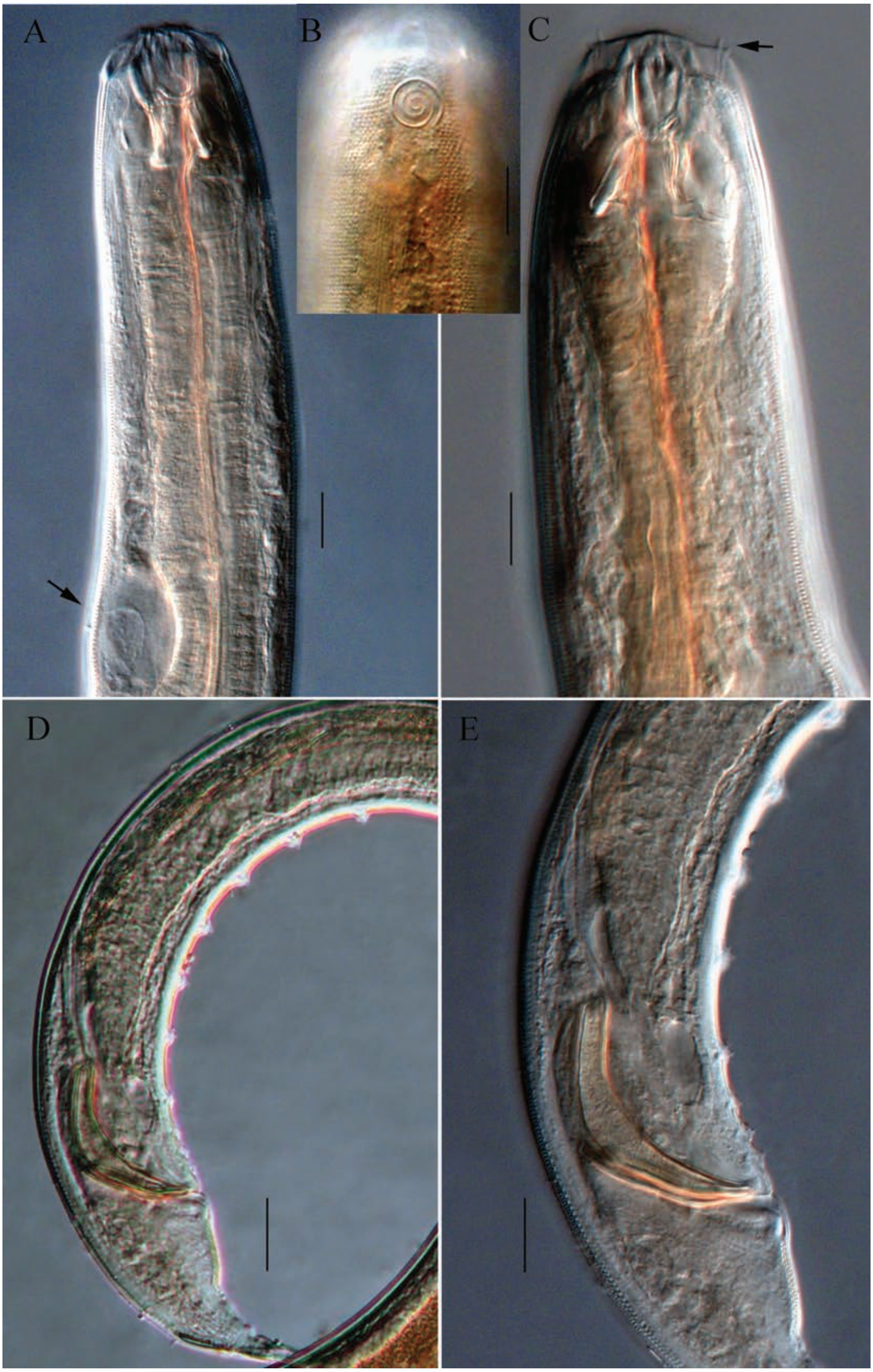


Figure 2. Microscopic images of *Halichoanolaimus sinensis* sp. nov. **A** anterior end of holotype, showing buccal cavity and excretory ampulla (arrow) **B** anterior end of male 2, showing amphidial fovea **C** anterior end of holotype, showing stomatorhabdions and anterior sensilla (arrow) **D** posterior part of holotype, showing supplements **E** cloacal region, showing spicules, gubernaculum and supplements. Scale bars: 20 µm (**A, B, C, E**); 30 µm (**D**).

Table 1. Individual measurements of *Halichoanolaimus sinensis* sp. nov. (in μm except for ratios; -, null).

Characters	Holotype	Paratypes	
	male	males (*N* = 3)	females (*N*= 2)
Total body length	2416	2197±59.0 (2138–2259)	2792±38.2 (2765–2819)
Maximum body diameter	66	72.3±2.1(70–74)	86.0±5.7 (82–90)
Head diameter	36	35.3±3.1 (32–38)	39.0±0.8 (37–41)
Length of outer labial sensilla	4	3.0±0 (3–3)	3.0±0.0 (3–3)
Depth of buccal cavity	46	36.0±2.6 (31–38)	40.0±0.0 (40–40)
Width of amphid	14	11.3±1.2 (10–12)	10.0±0.0 (10–10)
Amphid from anterior end	20	20.0±1.7 (19–22)	14.0±1.4 (13–15)
Nerve ring from anterior end	140	117±0 (117–117)	–
Length of pharynx	320	301.3±24.0 (274–319)	307.0±18.4 (294–320)
Body diameter at pharyngeal base	66	67.0±4.0 (63–71)	69.0±9.9 (62–76)
Spicule length along arc	82	79.7±5.5 (76–86)	–
Length of gubernaculum	42	45.0±5.3 (41–51)	–
Number of precloacal supplements	10	12.0±1.0 (11–13)	–
Vulva from anterior end	–	–	1251.5±153.4 (1143–1360)
V%	–	–	44.8±4.9 (41.3–48.2)
Body diameter at cloaca	55	55.3±1.2 (54–56)	–
Tail length	166	190.7±7.6 (182–196)	204.0±2.8 (202–206)
a	36.6	30.4±1.3 (28.9–31.4)	32.6±2.6 (30.7–34.4)
b	7.6	7.3±0.8 (6.9–8.2)	9.1±0.4 (8.8–9.4)
c	14.6	11.5±0.8 (10.9–12.4)	13.7±0.0 (13.7–13.7)
c'	3.0	3.5±0.2 (3.3–3.6)	3.1±0.4 (2.8–3.4)

half cylindrical portion. The new species is most similar to *H. sonorus* Belogurov & Fadeeva, 1980 in body shape and number of precloacal supplements, but differs from the latter species by numbers of amphid turns (2.5–3 vs 4–4.2), different shape and structure of spicules (spicules without capitulum, distal hook and central spacer vs with weak capitulum, distal hook and central spacer). The new species is also similar to *H. stagnalis* Gagarin & Long, 2017 in the number of the amphidial turns and tail, but can easily be distinguished from the latter by the different arrangement of precloacal supplements (3 posterior supplements smaller and closer vs 5–6 smaller and closer supplements

Halichoanolaimus zhangi **sp. nov.**

https://zoobank.org/CDC5A1AD-A09C-4716-A0DB-5D5336EE0B10
Figs 3–5, Table 2

Material examined. Two males and one juvenile were obtained. ***Holotype***: ♂1 on slide 22HSB-11-2-1; ***paratypes***: ♂2 and juvenile on slide 22HSB-11-2-2. Type specimens were deposited in the Marine Biological Museum of the Chinese Academy of Sciences, Qingdao.

Type locality and habitat. Holotype and paratypes were found from intertidal muddy sediment at Rizhao coast along the Yellow Sea; 35°18'N, 119°31'E; 0–2 cm sediment depth.

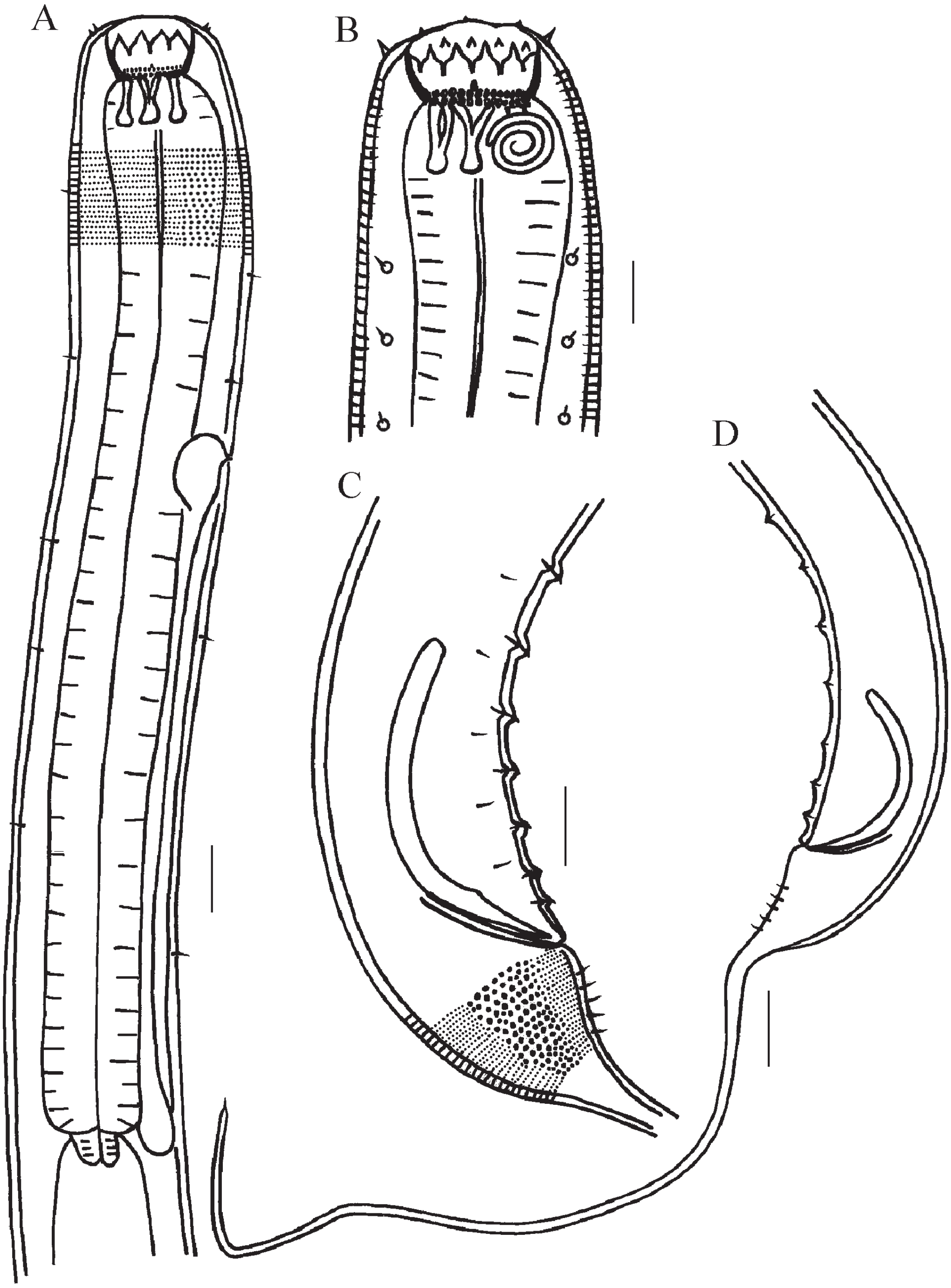


Figure 3. Drawings of *Halichoanolaimus zhangi* sp. nov. **A** pharyngeal region of holotype **B** anterior end of holotype **C** cloacal region of holotype **D** posterior end of male 2. Scale bars: 30 μm (**A, B, C**); 50 μm (**D**).

Etymology. The specific epithet "zhangi" is in honor of Professor Zhinan Zhang, a Chinese nematologist, in recognition of his contributions to nematode taxonomy.

Measurements. All measurement data are given in Table 2.

Description. Males. Body cylindrical, tapering slightly towards posterior end. Cuticle with transverse rows of punctations. Lateral differentiation presents except to anterior half of pharynx with even punctations. Lateral differentiation consisting of slightly larger and more widely spaced punctations. Four longitudinal rows of pore complexes situated at sublateral sides of pharyngeal region (Fig. 4B). Each row with 10–12 pores. Cephalic region slightly rounded.

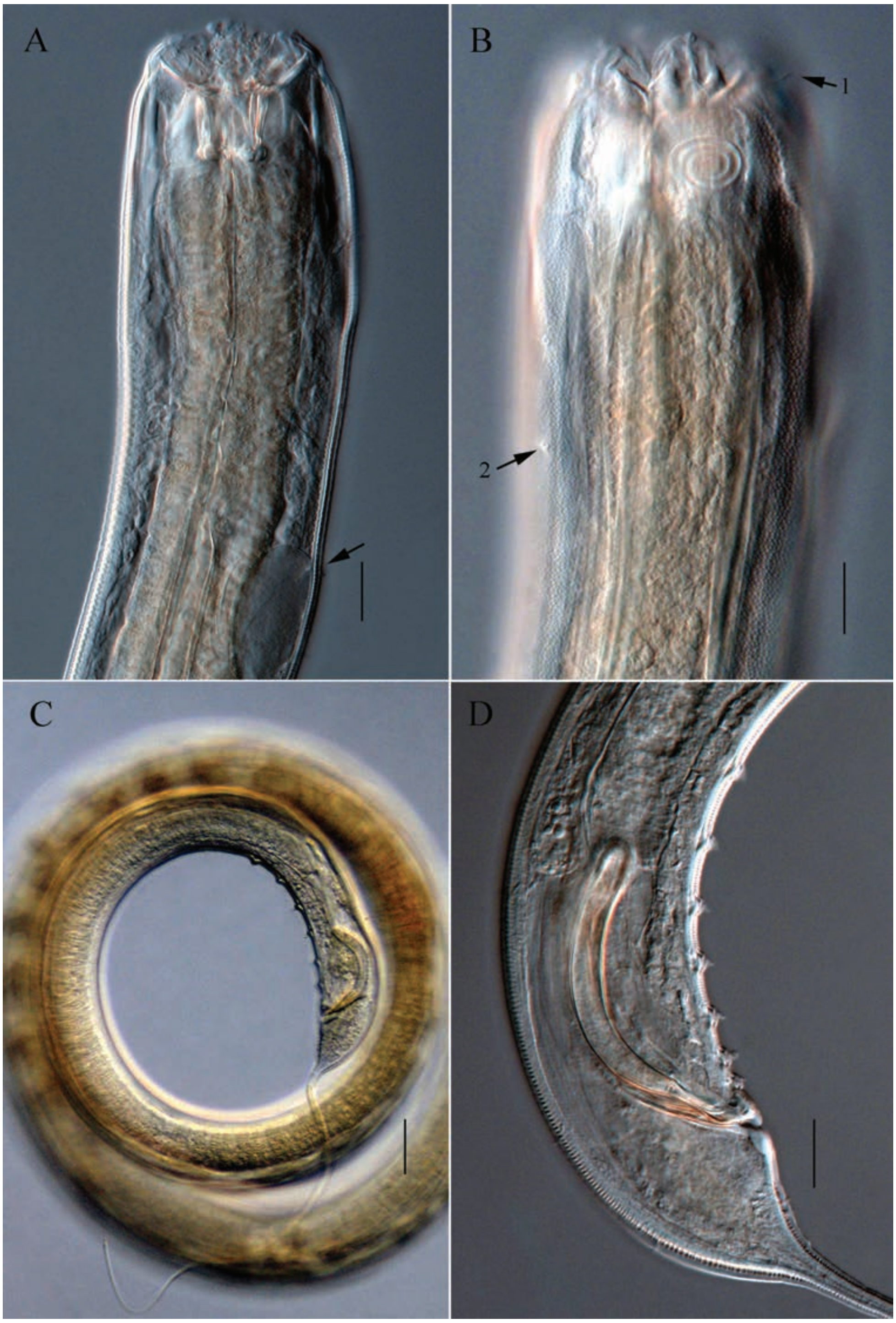


Figure 4. Microscopic images of *Halichoanolaimus zhangi* sp. nov. **A** anterior end of holotype, showing buccal cavity and excretory pore (arrow) **B** anterior end of holotype, showing cephalic seta (arrow 1) amphidial fovea and cuticle pores (arrow 2) **C** posterior portion of male 2, showing spicules and tail **D** cloacal region of holotype, showing spicules, gubernaculum and supplements. Scale bars: 20 µm (**A, B, D**); 50 µm (**C**).

Inner and outer labial sensilla papillose; four cephalic sensilla setiform, 4–5 µm long. Amphideal fovea multispiral with 3–3.25 turns, located at the level of the buccal cavity base, 27–28 µm from anterior end of body. Buccal cavity large, 43–45 µm deep, divided into anterior and posterior portions by two rows of 25 denticles. Anterior portion of buccal cavity cup-shaped, with three sets of three

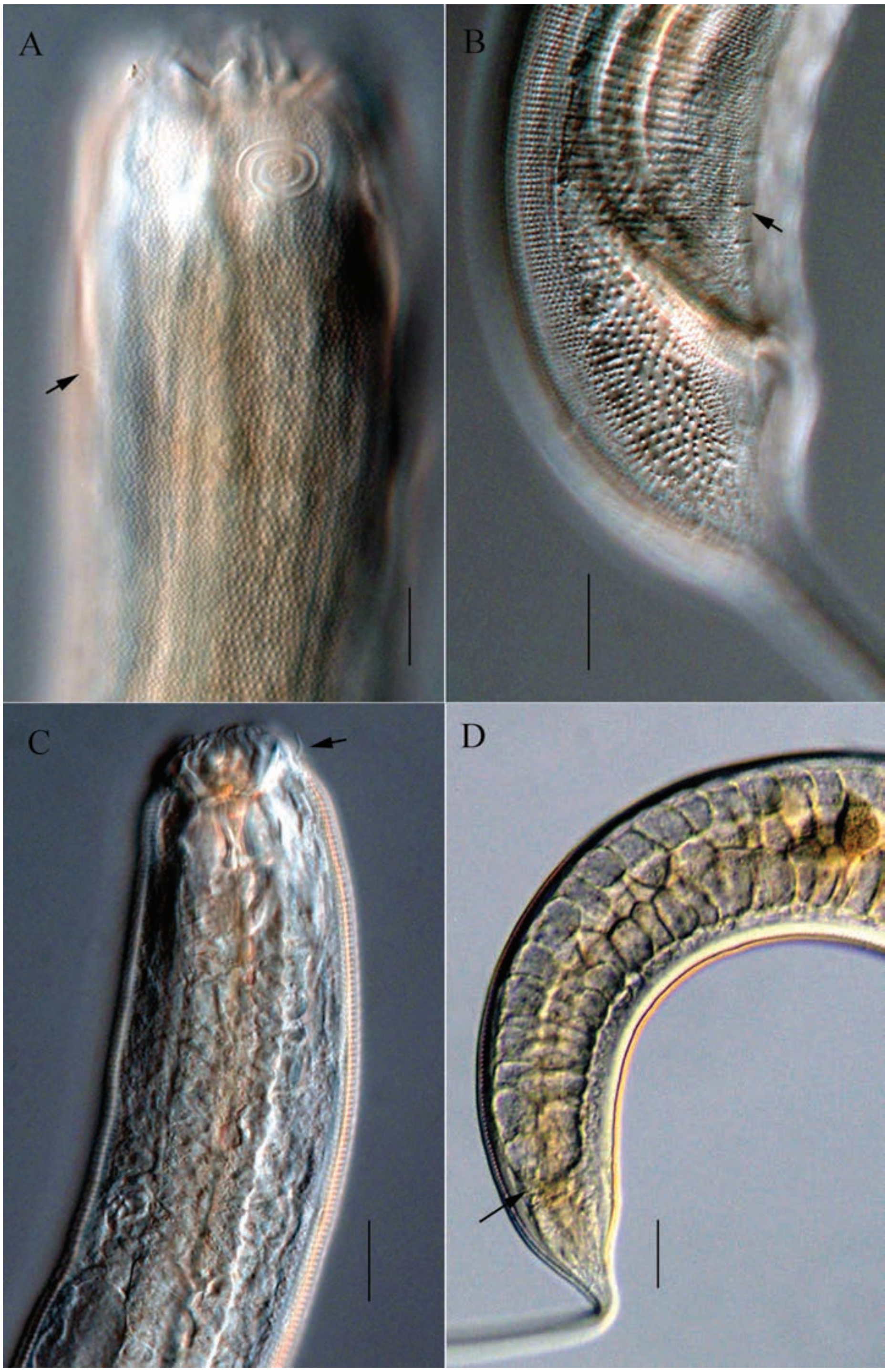


Figure 5. Microscopic images of *Halichoanolaimus zhangi* sp. nov. **A** anterior end of holotype, showing lateral differentiation and somatic setae (arrow) **B** cloacal region of holotype, showing lateral differentiation and conical setae situated at two subventral sides of precloacal supplements (arrow) **C** anterior end of juvenile, showing buccal cavity and cephalic sensilla (arrow) **D** posterior portion of juvenile, showing the end of intestine (arrow). Scale bars: 20 μm (**A, B, C, D**).

cuticularized rhabdions, terminating in three sets of paired denticles; posterior portion of buccal cavity narrower, cylindrical, surrounded by three Y-shaped pairs of cuticularized rhabdions with swollen bases, ca 20 μm long. Pharynx cylindrical, muscular, without anterior or posterior bulb; pharyngeal lumen cuticularized. Nerve ring difficult to distinguish. Secretory-excretory system present.

Table 2. Individual measurements of *Halichoanolaimus zhangi* sp. nov. (in µm except for ratios; -, null).

Characters	Holotype	Paratypes	
	♂1	♂2	Juvenile
Total body length	3090	3075	1940
Maximum body diameter	80	79	62
Head diameter	63	60	35
Length of cephalic sensilla	5	4	5
Depth of buccal cavity	43	45	32
Width of buccal cavity	32	31	22
Width of amphid	20	18	12
Amphid from anterior end	27	28	21
Length of pharynx	483	474	332
Body diameter at pharyngeal base	78	76	60
Spicule length along arc	115	106	–
Length of gubernaculum	42	40	–
Number of precloacal supplements	7	7	–
Body diameter at cloaca	58	52	–
Tail length	630	590	314
a	38.6	38.9	31.3
b	6.4	6.5	5.8
c	4.9	5.2	6.2
c'	10.9	11.3	9.2

Ventral gland small, situated at level of cardia; ampulla large, excretory pore situated at position of three corresponding body diameters from the anterior end. Cardia small, partially surrounded by intestine.

Reproductive system diorchic with two opposed, outstretched testes. Anterior testis to the right or ventrally to intestine, posterior testis to the left side of intestine. Spicules paired, curved, gradually narrowing from proximal to distal end with pointed tip, ca 2 cloacal body diameters long. Gubernaculum rod-like, adjoining to the dorsal side of spicules. 7 papilliform precloacal supplements, the most posterior supplement located 14 µm from the cloaca; remaining supplements gradually increasing the spacing distance forward, from 9 µm to 26 µm to each other. Each supplement consists of conical papilla and an internal duct. Two rows of short conical setae situated at two subventral sides of the precloacal supplements region of body. Tail conical with a long posterior filiform portion, accounts for 92% total tail length. A row of 5 caudal setae distributed at ventral side of tail conical part, 3–4 µm long. Caudal glands and spinneret present, 7 µm long.

Female not found. Juvenile similar to males in body shape, and with a long filiform tail, except body size smaller, intestine with blind end.

Differential diagnosis and discussion. *Halichoanolaimus zhangi* sp. nov. is distinct by lateral differentiation presenting posterior to the middle of the pharynx, amphideal fovea with 3.0–3.3 turns, spicules curved, gradually narrowing from proximal to distal end with pointed tip, 7 papilliform precloacal supplements, gradually increasing the spacing distance forward, two rows of subventral stout setae situated at precloacal region, tail elongated, filiform. The new species is most similar to *H. possjetiensis* Belogurov & Fadeeva, 1980 in the filiform tail and number of precloacal supplements, but differs from the latter species by body slender (a=38.6–38.9 vs body stout, a=25.8–26.6), longer tail (c=4.9–5.2 vs c=8–8.3) and different gubernaculum (slender and straight vs. broad and hooked proximally in *H. possjetiensis*).

Updated key to valid species of *Halichoanolaimus* (based on Zograf et al. 2015)

1 Tail consists of anterior conical and posterior filiform parts **2**
– Tail with conical or finger-shaped (not filiform) posterior part **25**
2 Index F (ratio of the filiform portion to the total tail length) ≤ 75% **3**
– Index F ≥ 80%.. **16**
3 More than 5 amphid turns **4**
– Equal to or less than 5 amphid turns **7**
4 5.5 amphid turns, 4 precloacal supplements .... ***H. macrophallus***
– 6.0–6.5 amphid turns, 3 or 5 precloacal supplements **5**
5 5 precloacal supplements .... ***H. brandtae***
– 3 precloacal supplements **6**
6 6.0 amphid turns, index c' > 5.2 .... ***H. anisospermus***
– 6.5 amphid turns, index c'=4.7.. ***H. pumilus***
7 4.5–5.0 amphid turns... **8**
– 3.0–4.2 amphid turns.. **11**
8 6–8 supplements **9**
– 2–4 supplements **10**
9 c'=3.6, spicules 60 µm long .... ***H. ovalis***
– c'=5.1–6.3, spicules 97 µm long.. ***H. funestus***
10 c'=3.7–5.2, spicules 43 µm long.. ***H. consimilis***
– c'=2.4–3.2, spicules 56–59 µm long...................................... ***H. ossilagulus***
11 3–6 posterior-most precloacal supplements smaller and closer to each other than remaining supplements **12**
– All precloacal supplements almost equal in size.................................... **14**
12 3.5–3.8 amphid turns, tail with 3/4 cylindrical portion.......... ***H. sicaoensis***
– 2–3 amphid turns, tail with 1/2–2/3 cylindrical portion........................... **13**
13 Posterior 5–6 supplements smaller and closer, spicules 72–74 µm .... ***H. stagnalis***
– Posterior 3 supplements smaller and closer, spicules 76–86 µm.............. .... ***H. sinensis* sp. nov.**
14 Amphid with 3.2 turns, 13 supplements, spicules 73 µm long..... ***H. unicus***
– Amphid with 3.5–4.2 turns, 11–12 supplements..................................... **15**
15 Spicules 83–100 µm, 12 supplements .... ***H. duodecimpapillatus***
– Spicules 63–75 µm, 11 supplements .... ***H. sonorus***
16 Index c = 3, male body less than 1 mm, supplements and stoma arm absent, spicules 20 µm long .... ***H. minutissimus***
– Index c > 3, males body longer than 1 mm, supplements present, stoma armed, spicules longer than 40 µm... **17**
17 Index c > 14, amphid with 1.5–2.0 turns.............................. ***H. raritanensis***
– Index c < 10, amphid with 2–7 turns **18**

18 Dotted denticles posterior to comb in stomatorhabdion, spicules longer than 90 μm **19**
– Dotted denticles absent, spicules shorter than 90 μm **21**
19 Buccal cavity armed with comb consisting of 10 denticles, 5 precloacal papillae .... ***H. balochiensis***
– Buccal cavity armed with comb consisting of more than 20 denticles, 7 precloacal papillae **20**
20 Body stout, a=26–27, c=8 .... ***H. possjetiensis***
– Body slender, a=39, c=5 .... ***H. zhangi* sp. nov.**
21 Amphidial fovea 40–50% cbd, precloacal supplements barely visible .... ***H. minor***
– Amphidial fovea less than 33% cbd, precloacal supplements prominent **22**
22 Comb of each stomatorabdion armed with 7 denticles .... ***H. lanceolatus***
– Comb of each stomatrhabdion armed with 9–15 denticles **23**
23 Spicules 48–56 μm long, 6–9 precloacal supplements .... ***H. dolichurus***
– Spicules longer than 70 μm **24**
24 Index F = 96%, 4 precloacal supplements .... ***H. chordiurus***
– Index F < 96%, 11–14 precloacal supplements***H. quattuordecimpapillatus***
25 Tail with finger-shaped posterior part .... ***H. macrospiculatus***
– Tail conical **26**
26 Amphidial fovea 60% cbd, with 6 turns .... ***H. norvegicus***
– Amphidial fovea more than 60% cbd, more or fewer than 6 turns **27**
27 Index c = 13, spicules 29 μm long .... ***H. robustus***
– Index c ≥ 16, spicules 50 μm or longer **28**
28 Index c = 17, 2 supplements, spicules 50 μm long .... ***H. caucasicus***
– Index c = 18–24, 5–14 supplements spicules 76–78 μm long **29**
29 5 supplements, spicules not cephalated, with groove in the posterior third .... ***H. lukjanovae***
– 13–14 supplements, spicules cephalated, without groove .... ***H. bispirae***

Acknowledgements

The authors are very thankful to Wen Guo for her kind help in sample collection. We are sincerely grateful to two anonymous referees for reviewing and improving the manuscript.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This research was funded by the Natural Science Foundation of Shandong Province (grant number ZR2022QC218).

Author contributions

Project Management, work program, methodology and taxonomy: M.H.; experiment, data collection: H. Z.; writing and editing of paper: M.H. All authors have read and agreed to the submitted version of the manuscript.

Author ORCIDs

Mian Huang https://orcid.org/0000-0003-3343-1520
Hongxiu Zhai https://orcid.org/0000-0003-0003-9549

Data availability

All of the data that support the findings of this study are available in the main text.

References

Allgén CA (1933) Freilebende Nematoden aus dem Trondhjemsfjord. Capita Zoologica 4(2): 1–162.

Allgén CA (1940) Über einige norwegische marine Tiefen-Nematoden. Folia Zoologica et Hydrobiologica 10: 258–281.

Bastian HC (1865) Monograph of the Anguillulidae, or Free Nematoids, Marine, Land, and Freshwater; with Descriptions of 100 New Species. Transactions of the Linnean Society of London XXV(Part II): 73–184. https://doi.org/10.1111/j.1096-3642.1865.tb00179.x

Belogurov OI, Fadeeva NP (1980) Notes on the Genus *Halichoanolaimus* (Nematoda, Choanolaimidae) with the Description of Two New Species. Zoologicheskii Zhurnal 59(5): 656–665.

Chitwood BG (1933) A revised classification of the Nematoda. The Journal of Parasitology. Papers in Helminthology, Ninth Annual Meeting 20(2): 115–148.

Chitwood BG (1951) North American marine nematodes. The Texas Journal of Science 3(4): 617–672.

Chu MD, Hao YD, Huang Y (2023) Descriptions of *Leptolaimus sinensis* sp. nov. and *Perspiria brevicaudata* sp. nov. (Nematoda) from the Yellow Sea, China. Zootaxa 5258(5): 524–536. https://doi.org/10.11646/zootaxa.5258.5.2

Cobb NA (1915) Nematodes and their relationships. United States Department of Agriculture—. Agricultural Research, 457–490.

Daschenko OI, Belogurov OI (1991) The morphology of free-living marine nematode *Halichoanolaimus bispirae* sp.n. (Nematoda, Chromadorida, Choniolaimidae) from polychaetes colony. In: Fadeev VI, Zvyagintsev, AY, Kubanin AA, Bagaveeva EV (Eds) Biological studies of benthos and fouling in the Sea of Japan. DVO AN USSR, Vladivostok, 98–104.

de Jonge VN, Bouwman LA (1977) A simple density separation technique for quantitative isolation of meiobenthos using the colloidal silica Ludox-TM. Marine Biology 42(2): 143–148. https://doi.org/10.1007/BF00391564

de Man JG (1886) Anatomische Untersuchungen über freilebende NordseeNematoden. Paul Frohberg, Leipzig, 82 pp.

Ditlevsen H (1921) Papers from Dr. Th. Mortensens Pacific Expedition 1914–16. III Marine free-living Nematodes from the Auckland and Campbell Islands. Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i Kjøbenhavn 73: 1–39.

Gagarin V, Long P (2017) Description of two new species of free-living nematodes: *Halichoanolaimus stagnalis* sp. nov. and *Actinonema dolichurum* sp. nov. from

Artificial reservoirs in Vietnam. Amurian Zoological Journal 9(3): 131–142. https://doi.org/10.33910/1999-4079-2017-9-3-131-142

Gerlach SA (1955) Zur Kenntnis der freilebenden marinen Nematoden von San Salvador. Zeitschrift für wissenchaftliche Zoologie Band 158, Heft 2–4: 249–303.

Gourbault N, Vincx M (1985) Nématodes abyssaux (Campagne Walda du N/O “Jean Charcot”). V. Espèces nouvelles de Selachinematidae, dépourvues d’anus. Cahiers de Biologie Marine 26(1): 87–97.

Hao YD, Chu MD, Huang Y (2022) *Trefusia brevicauda* sp. nov. and *Conilia parasinensis* sp. nov. (Nematoda, Enoplida) from the Yellow Sea, China. Cahiers de Biologie Marine 63(3): 257–267.

Hasbrouck ER (1966) *Halichoanolaimus raritanensis* n. sp. (Chromadoroidea: Cyatholaimidae) from New Jersey. Proceedings of the Helminthological Society of Washington 33: 23–25.

Higgins RP, Thiel H (1988) Introduction to the Study of Meiofauna. Smithsonian Institution Press, Washington, D.C., 488 pp.

Hopper BE (1961) Marine nematodes from the coastline of the Gulf of Mexico. Canadian Journal of Zoology 39(2): 183–199. https://doi.org/10.1139/z61-023

Huang Y, Guo YQ (2022) Free-living marine nematodes from the East China Sea. Springer Nature Singapore Pte Ltd, Singapore, 1–409. https://doi.org/10.1007/978-981-16-3836-7

Inglis WG (1968). Annales de Parasitologie Humaine et Comparee 35: 190–191.

Inglis WG (1983) An outline classification of the phylum Nematoda. Australian Journal of Zoology 31(2): 243–255. https://doi.org/10.1071/ZO9830243

Leduc D (2020) New and known *Halichoanolaimus* de Man, 1886 species (Nematoda: Selachinematidae) from New Zealand’s continental margin. European Journal of Taxonomy 726: 59–82. https://doi.org/10.5852/ejt.2020.726.1175

Leduc D, Zhao ZQ (2016) Molecular characterisation of five nematode species (Chromadorida, Selachinematidae) from shelf and upper slope sediments off New Zealand, with description of three new species. Zootaxa 4132(1): 59–76. https://doi.org/10.11646/zootaxa.4132.1.5

McIntyre AD, Warwick RM (1984) Meiofauna techniques. In: Holme NA, McIntyre AD (Eds) Methods for the study of marine benthos. Blackwell Scientific Publications, Oxford, 217–244.

Miljutin DM, Gad G, Miljutina MM, Mokievsky VO, Fonseca-Genevois V, Esteves AM (2010) The state of knowledge on deep-sea nematode taxonomy: How many valid species are known down there? Marine Biodiversity 40(3): 143–159. https://doi.org/10.1007/s12526-010-0041-4

Sergeeva NG (1973) New Species of Free Living Nematodes from the Order Chromadorida in the Black Sea (Novye Vidy Svobodnozhivushchikh Nematod Chernogo Moria iz otriada Chromadorida). Zoologicheskii Zhurnal 52(8): 1238–1241.

Ssaweljev S (1912) Zur Kenntnis der freilebenden Nematoden des Kolafjords und des Relictensee Mogilnoje. Travaux de la Société (Impériales) des Naturalistes de Saint-Petersbourg 42(2–3): 108–126.

Tchesunov AV (2014) Order Chromadorida Chitwood, 1933. In: Schmidt-Rhaesa A. (Ed.) Handbook of Zoology. Gastrotricha, Cycloneuralia, Gnathifera. Volume 2. Nematoda. De Gruyter, 373–398. https://doi.org/10.1515/9783110274257.373

Timm RW (1954) A survey of the marine nematodes of Chesapeake Bay, Maryland. The Catholic University of America, Biological Studies 23: 70.

Timm RW (1961) The Marine Nematodes of the Bay of Bengal. Proceedings of the Pakistan Academy of Science 1(1): 25–88.

Turpeenniemi TA, Nasira K, Maqbool MA (2001) A New Genus, Five New and Five Known Species of Free-Living Marine Nematodes (Nematoda: Monhysterida, Chromadorida) from Arabian Sea of Pakistan. Pakistan Journal of Nematology 19(1 & 2): 1–31.

Vitiello P (1970) Nématodes libres marins des vases profondes du Golfe du Lion. II. Chromadorida. Tethys (Cornella de Llobregat) 2: 449–500.

Xiao Y, Guo YQ (2023) Three new free-living marine nematode species of *Subsphaerolaimus* Lorenzen, 1978, *Halichoanolaimus* de Man, 1886 and Belbolla Andrássy, 1973 from mangrove wetlands in Taiwan. Zootaxa 5361(3): 301–322. https://doi.org/10.11646/zootaxa.5361.3.1

Zograf J, Trebukhova Y, Pavlyuk O (2015) New deep-sea free-living marine nematodes from the Sea of Japan: the genera *Siphonolaimus* and *Halichoanolaimus* (Nematoda: Chromadorea) with keys to species identification. Zootaxa 3911(1): 63–80. https://doi.org/10.11646/zootaxa.3911.1.3

ZooKeys 1208: 275–313 (2024)
DOI: 10.3897/zookeys.1208.113603

Research Article

Preliminary study of marine sponges (Porifera) in the littoral of Spermonde Archipelago, Indonesia

Singgih Afifa Putra[1,2], Rohani Ambo-Rappe[3], Jamaluddin Jompa[3], Nicole J. de Voogd[4,5]

1 Universitas Hasanuddin, Fakultas Ilmu Kelautan dan Perikanan, Program Doktor Ilmu Perikanan, Makassar 90245, Sulawesi Selatan, Indonesia
2 Balai Pengembangan Penjaminan Mutu Pendidikan Vokasi Bidang Kelautan Perikanan Teknologi Informasi dan Komunikasi (BPPMPV KPTK), Gowa 92172, Sulawesi Selatan, Indonesia
3 Universitas Hasanuddin, Fakultas Ilmu Kelautan dan Perikanan, Program Studi Ilmu Kelautan, Makassar 90245, Sulawesi Selatan, Indonesia
4 Naturalis Biodiversity Center, Understanding Evolution Group, 2333 CR Leiden, Netherlands
5 Leiden University, Institute of Biology Leiden (IBL), Sylviusweg 72, 2333 BE Leiden, Netherlands
Corresponding author: Singgih Afifa Putra (singgihafifa@gmail.com)

Abstract

Previous ecological studies show higher sponge diversity in the Spermonde Archipelago, SW Sulawesi, Indonesia, compared to the World Porifera Database. This study aims to provide an updated checklist of sponges of the Spermonde Archipelago, focusing particularly on the littoral area. Systematic sampling was executed through several observations, with roving techniques, e.g., snorkeling and SCUBA diving. In situ photographs of living sponges were taken using an underwater digital camera. Some specimens were collected and stored at the Naturalis Biodiversity Center, Leiden. Fragments of samples were analyzed using light and scanning electron microscopy. A total of 27 sponges (Calcarea and Demospongiae) were catalogued from the littoral area of the Spermonde Archipelago. Some of these are new records for the Sulawesi Sea/Makassar Strait marine ecoregion, including four potentially novel taxa. Preliminary morphological descriptions of all examined samples are presented. This study highlights the sponge assemblage flourishing in a shallow area characterized by a paucity of live corals and a predominant environment by macroalgae, rocks, and rubble.

Key words: Calcarea, Demospongiae, Indo-Pacific, taxonomy, turbid habitats

OPEN ACCESS

Academic editor: Fedor Konstantinov
Received: 22 October 2023
Accepted: 8 May 2024
Published: 1 August 2024

ZooBank: https://zoobank.org/B6DB2AC5-8878-471C-876E-207490E3A4D4

Citation: Putra SA, Ambo-Rappe R, Jompa J, de Voogd NJ (2024) Preliminary study of marine sponges (Porifera) in the littoral of Spermonde Archipelago, Indonesia. ZooKeys 1208: 275–313. https://doi.org/10.3897/zookeys.1208.113603

Introduction

The Spermonde Archipelago is located between the south-western part of Sulawesi and the Makassar Strait in Indonesia (Kench and Mann 2017). This region is placed in the Sulawesi Sea/Makassar Strait (SS/MS) marine ecoregion based on Marine Ecoregions of the World (Spalding et al. 2007). The whole archipelago consists of many coral cays and small islands (Umbgrove 1928; Kench and Mann 2017), with the highest coral cover less than 60% (Sari et al. 2021). The coral reef is the richest ecosystem with high species diversity (Cairns 1999; Williams et al. 2019; Kusumoto et al. 2020). Every part of the reef is influenced by different regimes of wave actions, light intensity, bathymetric range, and water currents (Kench and Mann 2017). The sponge community is one of the essential components of the reef environment (Rützler 2004), showing a wide distribution across the Spermonde Archipelago (de Voogd et al. 1999). This community is also recognized as comprising predominantly niche specialists with marked habitat preferences in coral reef ecosystems (Hooper 2008).

Numerous studies have been conducted on this archipelago due to its geological, biodiversity, and ecological significance in marine biology (Polónia et al. 2015). Taxonomic studies on sponge diversity in this region were sporadic. The sponge fauna within the SS/MS marine ecoregion is relatively well studied only in north Sulawesi (de Voogd et al. 2024). Only a few papers have conducted morphological taxonomic studies to describe new species or revise specific group of sponges (e.g., genus, family, or order), with a mention of the Spermonde Archipelago as a locality (de Weerdt and van Soest 2001; de Voogd 2004; Becking 2013; Alvarez et al. 2016; van Soest et al. 2021).

Globally, more than 9,000 sponge species are currently described (de Voogd et al. 2024). Taxonomic misidentifications by non-taxonomists are common when dealing with sponges (Cárdenas et al. 2022). Some comprehensive inventories of the sponge fauna from Indonesia have been published (van Soest 1990; Calcinai et al. 2017), including specific sponge category-based inventories (de Voogd and van Soest 2002; Calcinai et al. 2005; van Soest and de Voogd 2015; van Soest et al. 2021). However, sponge diversity across the Indonesian Archipelago is still considered underestimated (Calcinai et al. 2017; Putra et al. 2023).

According to the World Porifera Database (de Voogd et al. 2024), sponge diversity in the Sulawesi Sea/Makassar Strait marine ecoregion comprises 128 species, i.e., 17 species of Calcarea, 97 species of Demospongiae,13 species of Hexactinellida, and one species of Homoscleromorpha. The class Demospongiae is predominantly represented by the order Poecilosclerida, comprising 31 species. However, the latest ecological study reveals a higher sponge species beta diversity in the Spermonde Archipelago, SW Sulawesi. At least 151 species belonging to 68 genera and 37 families were identified in this area (de Voogd et al. 2006). Therefore, taxonomic studies are needed to describe the unregistered sponge species and elucidate the sponge alpha diversity in this marine ecoregion.

The current study is focused on the littoral area of the archipelago. This area is below the lowest tide, but including the reef flat. Reef flats are the most recent expression of sea-level coral reef growth (Hopley 2011). This area presents extreme conditions for coral reefs due to marginal environmental factors (Burt et al. 2020). Furthermore, the coral reef ecosystem in this shallow area, particularly in the inner zone of the archipelago, was reported to be in a very poor condition, ≈ 5–14% (Parenden et al. 2021; Sari et al. 2021). This habitat is dominated by dead corals with algae, macroalgae, and sediment cover (Parenden et al. 2021).

This study aims to provide preliminary morphological identifications of sponge specimens from the Spermonde Archipelago to fill the knowledge gap concerning marine sponge diversity of Indonesia. Additionally, it seeks to promote the study of sponge taxonomy in Indonesia and to update the checklist of sponge diversity of this marine ecoregion.

Materials and methods

Specimen collection

The specimen collection was conducted through several observations of the littoral area of the Spermonde Archipelago, Indonesia. Some observations were made by NJdeV in 2018, and by SAP during 2020 and 2021 (Fig. 1, Suppl. material 1). The observations were performed using a roving technique (Pattengill-Semmens 2001) through snorkeling or SCUBA Diving. Roving time is 1–2 hours within ≈ 90 m^2 for each site. The timed survey method does not provide density and abundance data but is most useful when the study aims to assess biodiversity (Reimer et al. 2018; Montano et al. 2020).

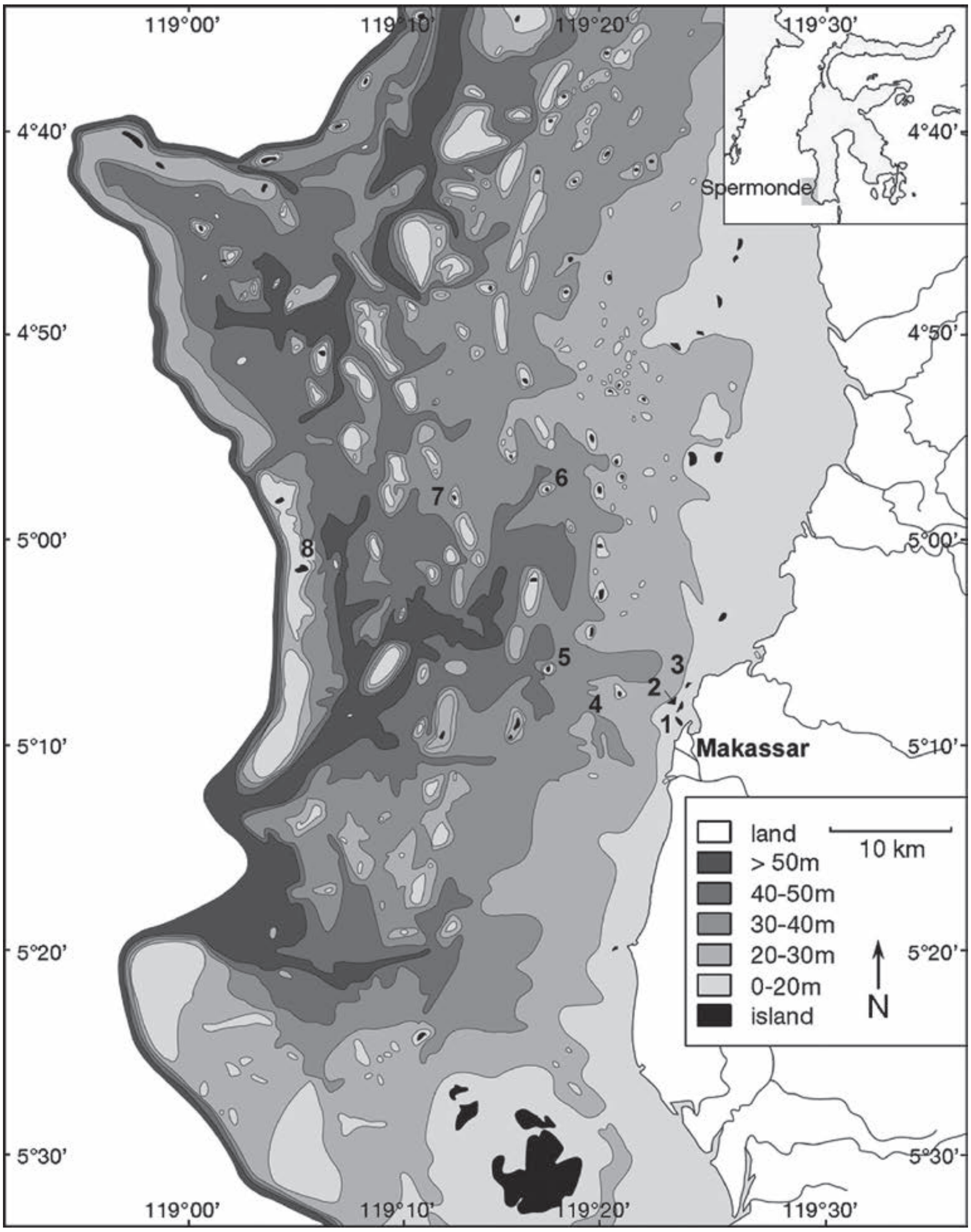


Figure 1. The location of sponge observation in the shallow-subtidal area of the Spermonde Archipelago, SW Sulawesi, Indonesia, i.e., 1) Lae-lae, 2) Gusung (as Gusung Tallang), 3) Kayangan, 4) Samalona, 5) Kudingarengkeke, 6) Badi, 7) Lumulumu, 8) Langkai.

Photographs of living sponges at the study site (in situ) were captured using an underwater digital camera (Nikon Coolpix W300 and Olympus TG-series). The specimens were immediately transferred into 96% ethyl alcohol for preservation during observation (Hooper 2003), and some of them were deposited in the museum collection of the Naturalis Biodiversity Center, Leiden, The Netherlands (**NBC**); the others are located at Balai Pengembangan Penjaminan Mutu Pendidikan Vokasi Bidang Kelautan Perikanan Teknologi Informasi dan Komunikasi (**BPPMPV KPTK**) in Gowa, Sulawesi Selatan.

Specimen identification

Fragments of sponges and sections of the skeleton were prepared and then examined using light microscopy (Leica DM5500 B and Olympus BX53) and JEOL Scanning Electron Microscope (JSM-6480LV) at the Naturalis Biodiversity Center, Leiden, following standard procedures for skeleton and spicule analysis (Rützler 1974; Boury-Esnault and Rützler 1997; Hooper 2003). Except for macro morphologies, which were measured with a vernier caliper, microscopic characteristics were assessed using Olympus cellSens Standard and Leica LAS Core software. Images were cleaned up and assembled in composite figures using Adobe Photoshop 2023 and Adobe Illustrator 2023 licensed to SAP. Measurements of spicules (smallest-largest-(mean)) rely on a minimum of 20 measurements of length and thickness for each type of spicule in the case of one or a few specimens. Systematic treatment refers to the description of Porifera morphological identification (Hooper and van Soest 2002) and the World Porifera Database/WPD (de Voogd et al. 2024). The recording of species names includes as much information as possible, such as valid names, species location, specimen description, and other taxonomic notes.

Results

Systematics

Accepted names, all synonyms, and systematic updates were based on the World Porifera Database (de Voogd et al. 2024), and all terminology follows updated terms (Boury-Esnault and Rützler 1997; Łukowiak et al. 2022).

Phylum Porifera Grant, 1835
Class Calcarea Bowerbank, 1862
Subclass Calcinea Bidder, 1898
Order Clathrinida Hartman, 1958
Family Clathrinidae Minchin, 1900
Genus *Clathrina* Gray, 1867

***Clathrina rodriguesensis* van Soest & de Voogd, 2018**
Fig. 2

Diagnostic features. In its natural environment, the species forms a large, encrusting mass composed of wide, closely linked tubes showing little variation in diameter. According to van Soest and de Voogd (2018), it can

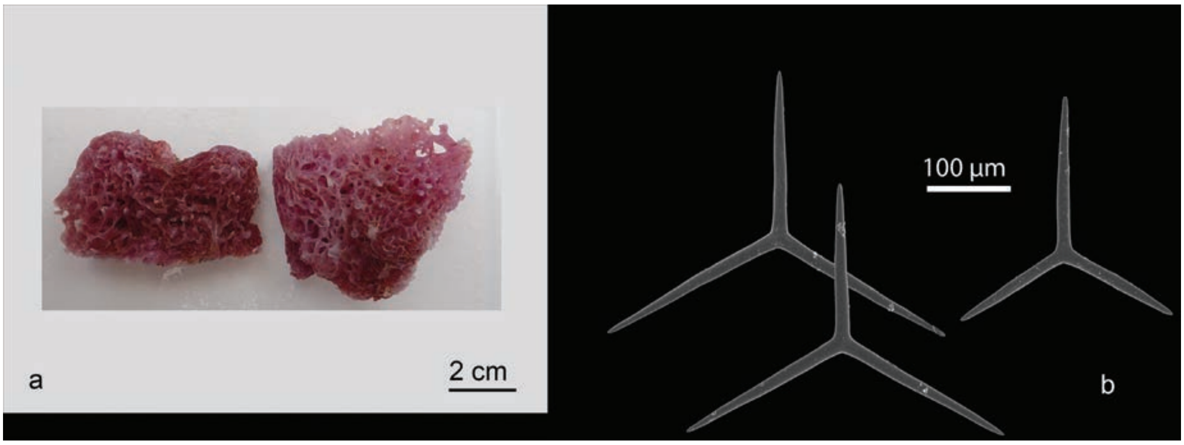


Figure 2. *Clathrina rodriguesensis* van Soest & de Voogd, 2018 from Kudingareng keke Island, the Spermonde Archipelago (Sample CEL035) **a** habitus of fresh specimen (photograph by NJdeV) **b** SEM image of the triactines.

spread flatly across wide areas, with the tubes arranged like a ladder. The main tubes often end in an opening slightly raised from the mass. The color is white with shades of blue, grey, or pink, turning pale beige or brown when preserved. Consistency firm and with asconoid aquiferous system. Spicules are only triactines.

Distribution and ecology. Previously, this species only recorded from Seychelles, Western Indian Ocean (van Soest and de Voogd 2018). This is first record for Indonesia (Kudingareng keke, the Spermonde Archipelago; reef flat).

Genus *Janusya* Klautau et al., 2021

Janusya tubuloreticulosa (van Soest & de Voogd, 2015)

Fig. 3

Diagnostic features. An orange flattened mass of short oscular tubes, connected at the substratum by a basal tubular network, the erect tubes maybe divided into one or two side tubes. The walls of tubes are thin with spicules are dominated by triactines. Triactines predominantly equiactinal with size 14.93–120.79 (83.54) × 3.39–6.76 (5.48) µm (n = 20). Tetractines are also not rarely found with size 28.04–103.79 (83.77) × 4.98–5.94 (5.48) µm (n = 11).

Distribution and ecology. Originally reported from Ternate (van Soest and de Voogd 2015). First record from Samalona Island, the Spermonde Archipelago; reef flat.

Family Leucaltidae Dendy & Row, 1913
Genus *Laucaltis* Haeckel, 1872

Leucaltis nodusgordii (Poléjaeff, 1883)

Fig. 4

Diagnostic features. The species forms a clathrate mass of interconnected (anastomosing) tubes with varying lengths and diameters. Individual tubes can reach up to 2.5 cm in length and have diameters of 2–8 mm (van Soest and de Voogd 2015). The tubes end in oscula, which can be as wide as the

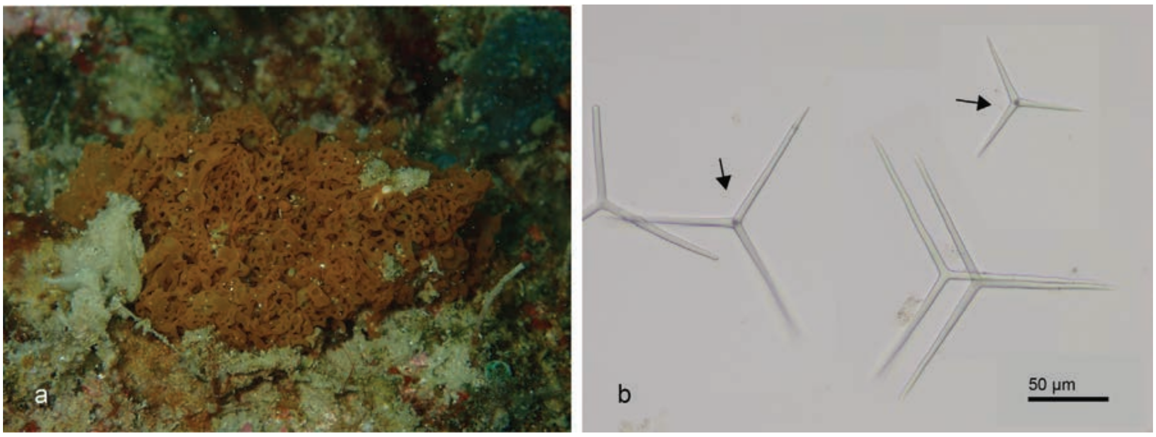


Figure 3. *Janusya tubuloreticulosa* (van Soest & de Voogd, 2015) from Samalona Island, the Spermonde Archipelago (Sample CEL001) **a** habitus in situ at Samalona reefs (photograph by NJdeV) **b** LM images of spicules, triactines and tetractines (arrows).

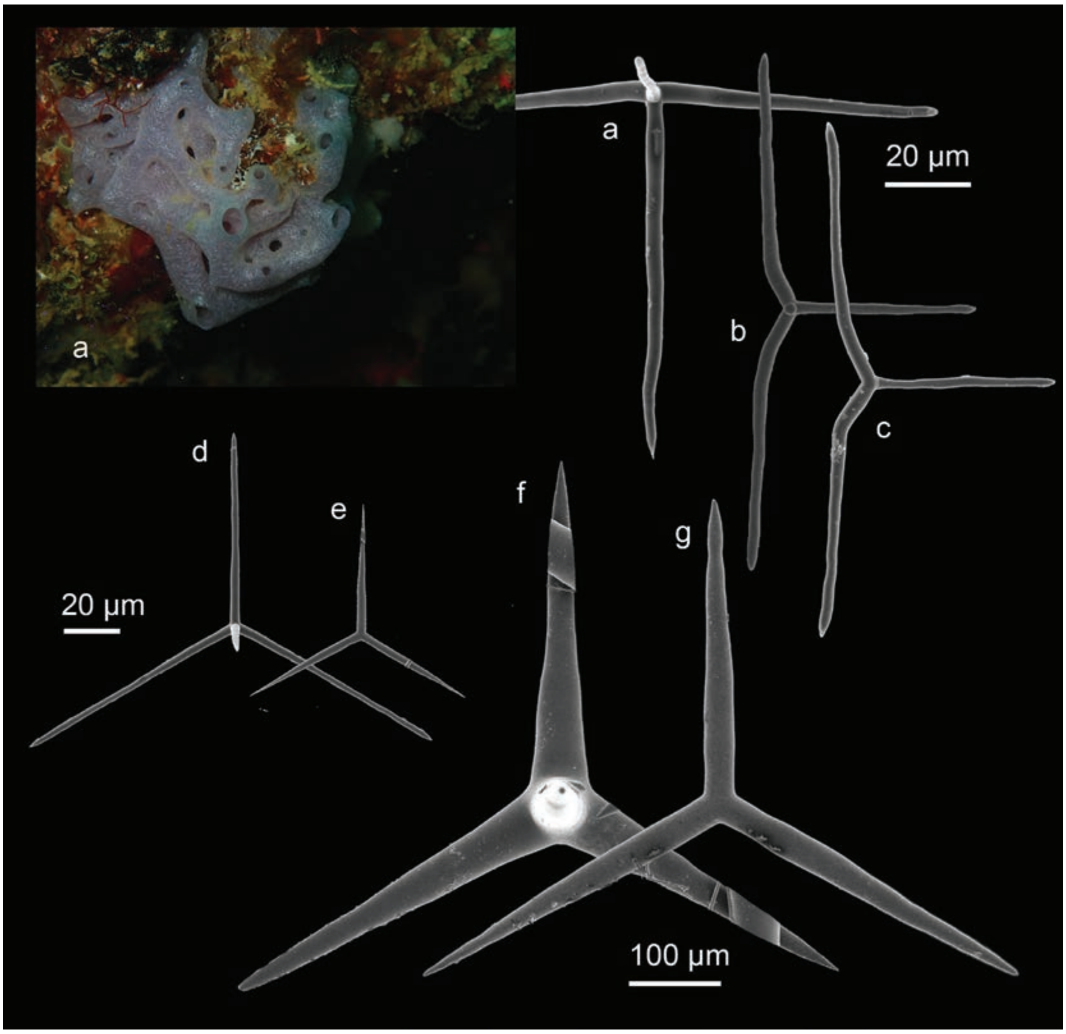


Figure 4. a habitus in situ *Leucaltis nodusgordii* (Poléjaeff, 1883) (CEL005) from Samalona Island, the Spermonde Archipelago (photograph by NJdeV). SEM images of spicules **a** regular equiangular tetractine of the chamber laye **b** 'Abruptly angled' tetractines **c** 'Abruptly angled' triactines (**b, c** both from the atrial region) **d** Small regular-shaped tetractines of the chamber layer **e** small regular-shaped triactines of the cortical region **f** Giant sized tetractines **g** giant sized triactines (**f, g** both from the cortical region).

tube itself (standing upright) or smaller (flush with the surface), and these oscula are naked. The surface is smooth, and the texture is brittle yet somewhat compressible. The color is white or pinkish white, sometimes lavender-colored, and it turns yellowish white when preserved. The cortical skeleton is formed by the basal triradiate system of giant tetractines mixed with giant triactines. Actines of the giant tetractines and triactines protrude into the choanosomal skeleton. Next to the actines of the giant tri- and tetractines, the choanosomal skeleton contains scattered intermediate to small-sized regular triactines and tetractines (see van Soest and de Voogd 2015 for detail description).

Distribution and ecology. *Leucaltis nodusgordii* is a new record for the Spermonde Archipelago (Samalona Island); reef flat. This species has been reported previously from north Sulawesi (van Soest and de Voogd 2015).

Class Demospongiae Sollas, 1885
Subclass Heteroscleromorpha Cárdenas et al., 2012
Order Clionaida Morrow & Cárdenas, 2015
Family Spirastrellidae Ridley & Dendy, 1886
Genus *Spirastrella* Schmidt, 1868

***Spirastrella* aff. *decumbens* Ridley, 1884**
Fig. 5

Diagnostic features. A thin encrusting sponge with a soft texture and a smooth surface. The living specimens exhibit a salmon-pink or orangish color. The ectosome of the sponge contains numerous microscleres (spirasters), forming the characteristic tangential crust found in this genus. In the choanosome, the megascleres are irregularly arranged tylostyles with well-formed, usually spherical heads (Calcinai et al. 2006). Our specimen shows spirasters with ornamented rays (Fig. 5d) that are not mentioned in the Calcinai et al. (2006) report from Vietnam.

Distribution and ecology. This species is present in the Australian region, New Caledonia, the Philippines, and Vietnam. In Indonesia is recorded from Ambon; this is a first record for the Spermonde Archipelago (Langkai Island; reef flat).

Order Haplosclerida Topsent, 1928
Family Callyspongiidae de Laubenfels, 1936
Genus *Callyspongia* Duchassaing & Michelotti, 1864
Subgenus *Cladochalina* Schmidt, 1870

***Callyspongia* (*Cladochalina*) *johannesthielei* van Soest & Hooper, 2020**
Fig. 6

Diagnostic features. Lobate form and hard surface with numerous, raised, cone-shaped projections (pointed papillae). Several large oscula between ≈ 6–7 mm. Pink to red in living and pale yellow in alcohol. The skeleton is reticulate with a fiber tract. This species was described as *Spinosella elegans* Thiele, 1899 (junior secondary homonym of *Callyspongia* (*Cladochalina*) *ele-*

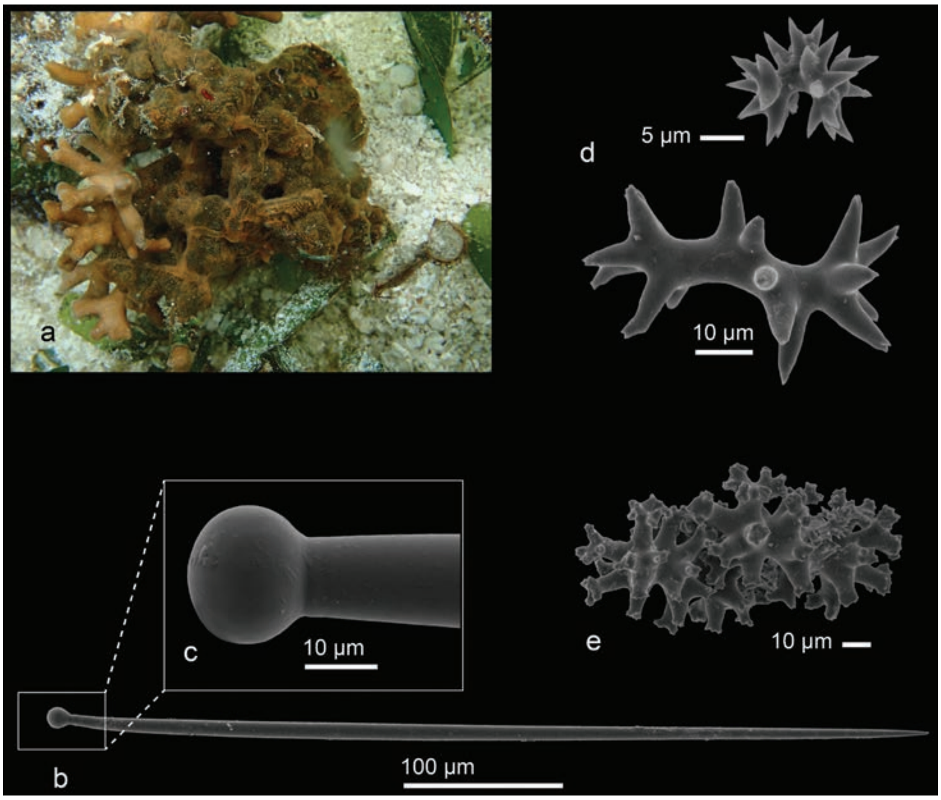


Figure 5. *Spirastrella* aff. *decumbens* Ridley, 1884, overgrowing coral skeleton **a** habitus in situ (CEL007) from seagrass bed of Langkai Island, the Spermonde Archipelago (photograph by NJdeV) **b** SEM image of tylostyle with **c** close up of the head **d** spirasters **e** spirasters with ornamented rays.

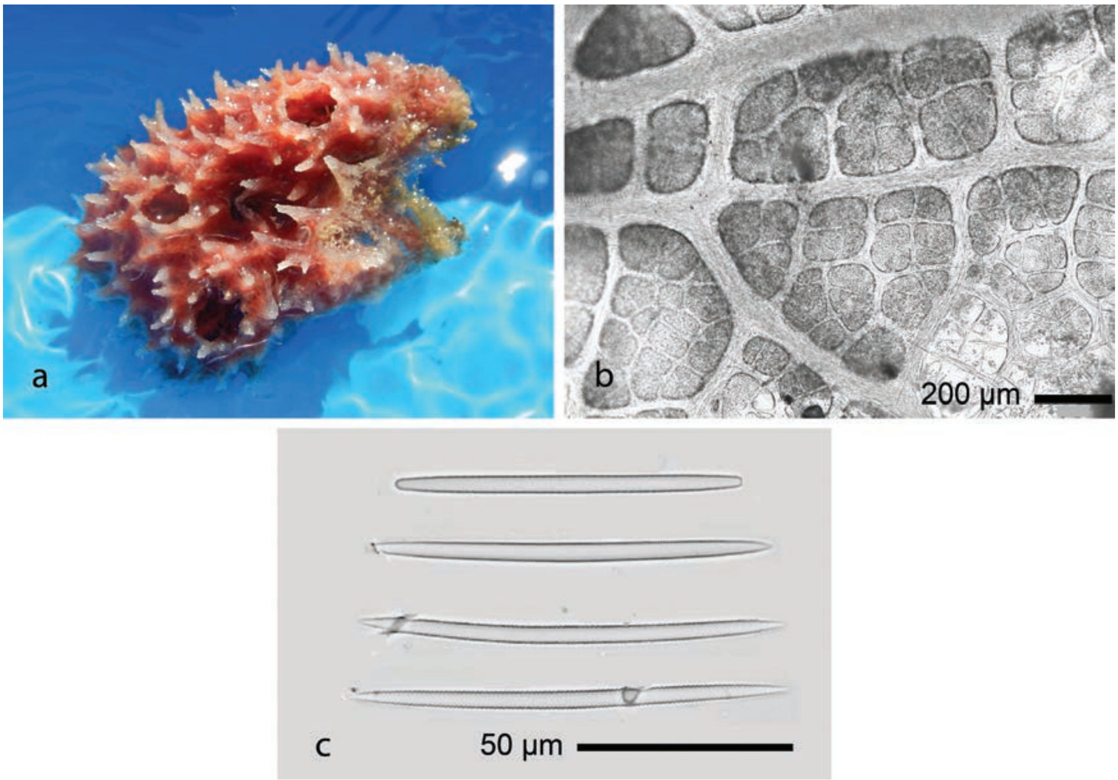


Figure 6. *Callyspongia* (*Cladochalina*) *johannesthielei* van Soest & Hooper, 2020 **a** habitus of fresh specimen (photograph by SAP) **b** skeleton **c** amphioxeas.

gans (von Lendenfeld, 1887)) as a large cup-shaped sponge, ≈ 30 cm high, hollow along its entire length, a pale brownish color when dry, and with very characteristic pointed papillae, often fused into a cluster of several, on the outer surface (Thiele 1899). The spicules of Thiele's species were shown as rather thin, short-tipped amphioxeas that are 90–100 µm × 3–5 µm (van Soest et al. 2020).

Distribution and ecology. Kema Bay (1°23'N, 125°04'E), north Sulawesi (Thiele 1899); and north-west of Samalona Island, the Spermonde Archipelago; reef flat; attached on rock.

Family Chalinidae Gray, 1867
Genus *Haliclona* Grant, 1841
Subgenus *Gellius* Gray, 1867

***Haliclona* (*Gellius*) *cymaeformis* (Esper, 1806)**
Fig. 7

Diagnostic features. The appearance is thickly encrusting to repent or arborescent (bushy). The specimen is hard and smooth on the surface, with a broad erect base with short branches. The color in life is dark greyish pink (dark purple) with desaturated dark green on the tips. After preservation, the color is pale pink to yellow. Ectosomal skeleton shows unispicular tract and covering the associated branching microalgae (Fig. 7c). Spicules are oxeas, 109–154 (129.7) × 2.3–5.2 (3.9) µm (*n* = 27), and microscleres are sigmas.

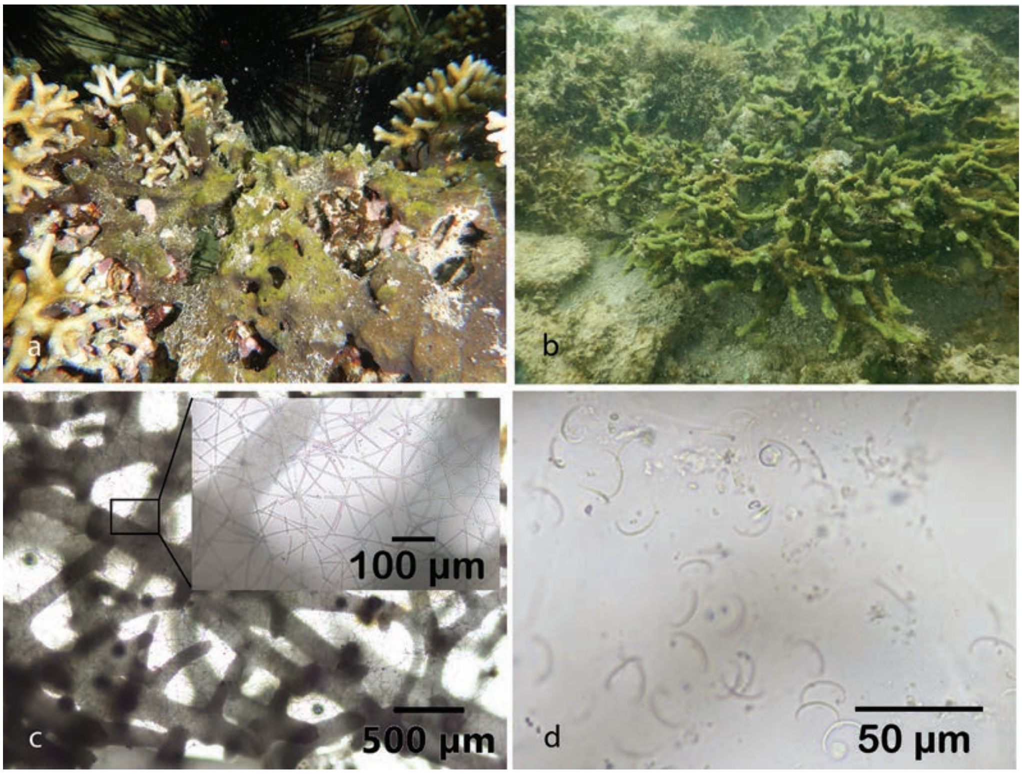


Figure 7. *Haliclona* (*Gellius*) *cymaeformis* (Esper, 1806) **a, b** habitus in situ at Samalona Island and Kayangan Island (respectively), the Spermonde Archipelago (all photographs by SAP) **c** LM images of tangential section showing Rhodophyta symbiont and unispicular tract (box) **d** sigmas.

Haliclona (*Gellius*) *cymaeformis* (Esper, 1806) was abundant in turbid water near Makassar City. This species is known to be associated with the rhodophyte *Ceratodictyon spongiosum* Zanardini, 1878 (Azzini et al. 2007). Its morphological appearance is possibly similar to those of *Halichondria* (*Halichondria*) *cartilaginea* (Esper, 1797) and *Callyspongia* (*Cladochalina*) *samarensis* (Wilson, 1925).

Distribution and ecology. This species has been recorded from marine karst lakes in Vietnam (Azzini et al. 2007), in shallow waters of the South China Sea (Huang et al. 2016; Lim et al. 2016), and in Taiwan (Li 2013), Andaman (Immanuel et al. 2015), India (George et al. 2020), across the Indonesian Archipelago (de Voogd and Cleary 2008), and north-west Australia (Fromont and Sampey 2014). Our samples were collected from a reef flat north-west of Samalona Island, overgrowing corals (*Seriatopora* sp. and *Acropora* sp.), also from Kayangan Island and Gusung Tallang; turbid reef environment.

Subgenus *Reneira* Schmidt, 1862

***Haliclona* (*Reniera*) *venusta* (Bowerbank, 1875)**
Fig. 8

Diagnostic features. Specimen form tube, soft and delicate. Color yellowish in living material and yellow to pale white in alcohol. The skeleton forms an isotropic reticulation of a single line spicules. All spicules on this specimen are oxeas, 88–109 (95.2) × 4.3–6.5 (5.7) μm (*n* = 20).

Distribution and ecology. The WPD checklist only lists four species of the subgenus *Reniera* recorded from marine ecoregions of Indonesia with two as doubtful species, *Haliclona* (*Reniera*) *cinerea* (Grant, 1826) (doubtful species), *Haliclona* (*Reniera*) *fascigera* (Hentschel, 1912), *Haliclona* (*Reniera*) *infundibularis* (Ridley & Dendy, 1887) (doubtful species), and *Haliclona* (*Reniera*) *venusta* (Bowerbank, 1875), but none of these species were registered in the Spermonde Archipelago (Putra et al. 2023). This report presents a new record of *Haliclona* (*Reniera*) *venusta* from the Spermonde Archipelago (Samalona Island; reef flat). Previously, this species has been only reported from Malacca Strait (Bowerbank 1875).

Subgenus *Soestella* de Weerdt, 2000

***Haliclona* (*Soestella*) *elegantia* (Bowerbank, 1875)**
Fig. 9a, d, e

Diagnostic features. Small specimen (l × w × h; 46 × 34 × 30 mm) and fragile, found growing in turbid water near the coastal city of Makassar. Massive shape with large oscula (3–4 mm in diameter). Color in life deep blue and pale white in alcohol. The choanosomal skeleton is paucispicular tracts. Spicules are oxeas, larger oxeas 163.9–196.2 (163.9) × 7–9.9 (8) μm (*n* = 20) and thin oxeas 92–156.1 (127.5) × 0.8–5.7 (3) μm (*n* = 26). Microscleres are sigmas. The subgenus *Haliclona* (*Soestella*) consists of 25 species,

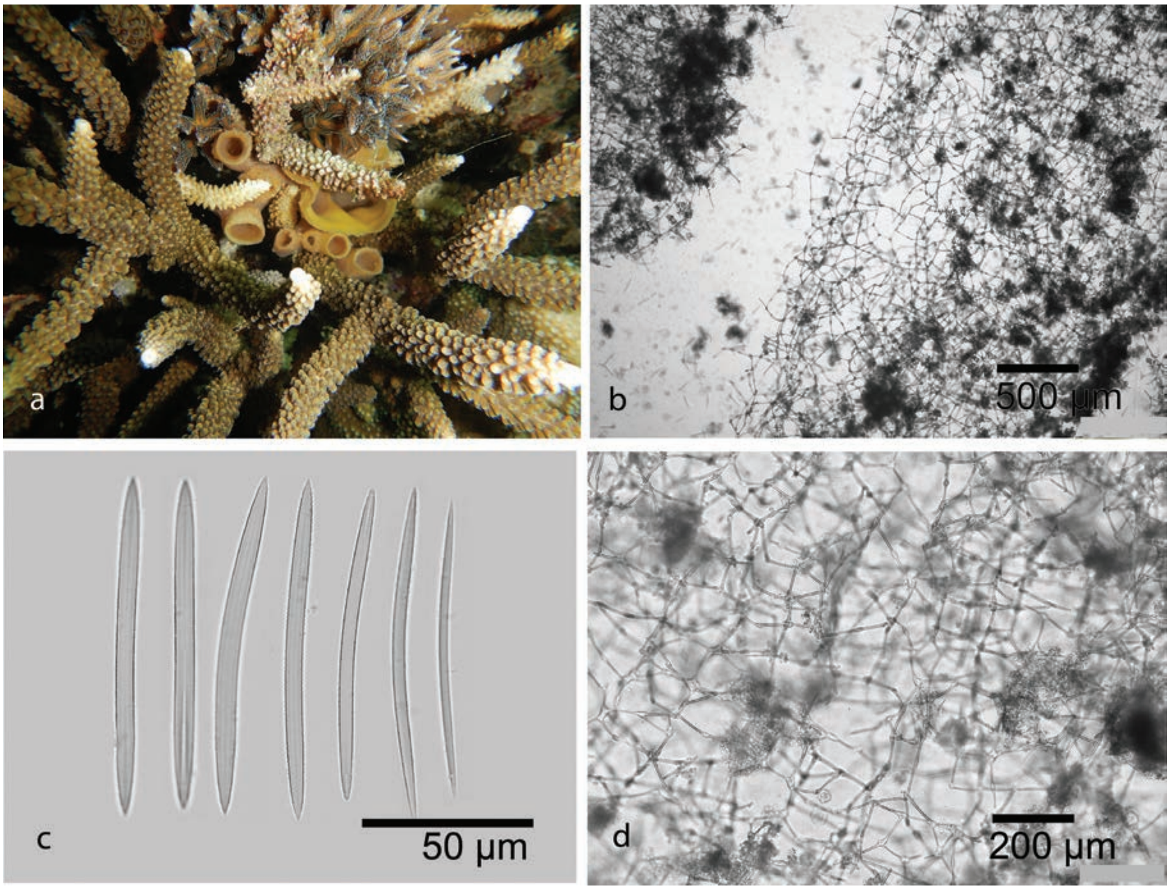


Figure 8. *Haliclona* (*Reniera*) *venusta* (Bowerbank, 1875) **a** habitus in situ at Samalona Island, the Spermonde Archipelago (photograph by SAP) **b** LM images of tangential section and spicules reticulation **c** oxeas **d** close up of spicules reticulation.

and only *Haliclona* (*Soestella*) *elegantia* is registered from the marine ecoregions of Indonesia (Putra et al. 2023). This species is poorly studied; in fact, we have found no studies after its original description. Bowerbank's description did not include an illustration, but the specimen was described as of small appearance and small spicules (short and stout) with fragile and elegant uni-, bi-, and tri-spiculous reticulation on the dermal structure (Bowerbank 1875: 286).

Distribution and ecology. Previously recorded from Malacca Strait (Bowerbank 1875). This is the first record for the Spermonde Archipelago (at Kayangan Island, and Gusung Tallang Island; turbid environment).

***Haliclona* (*Soestella*) sp. 1**

Fig. 9b

Diagnostic features. The specimen is fragile and shapeless (amorphous), the surface is slick and smooth; the color in life is mostly black, also in alcohol. Oscula present with 1–3 mm diameter. The spicule arrangements are oxeas 101–162 (128.8) × 1.5–7 (4.9) µm (n = 21).

Distribution and ecology. North-west Samalona Island, the Spermonde Archipelago; reef flat.

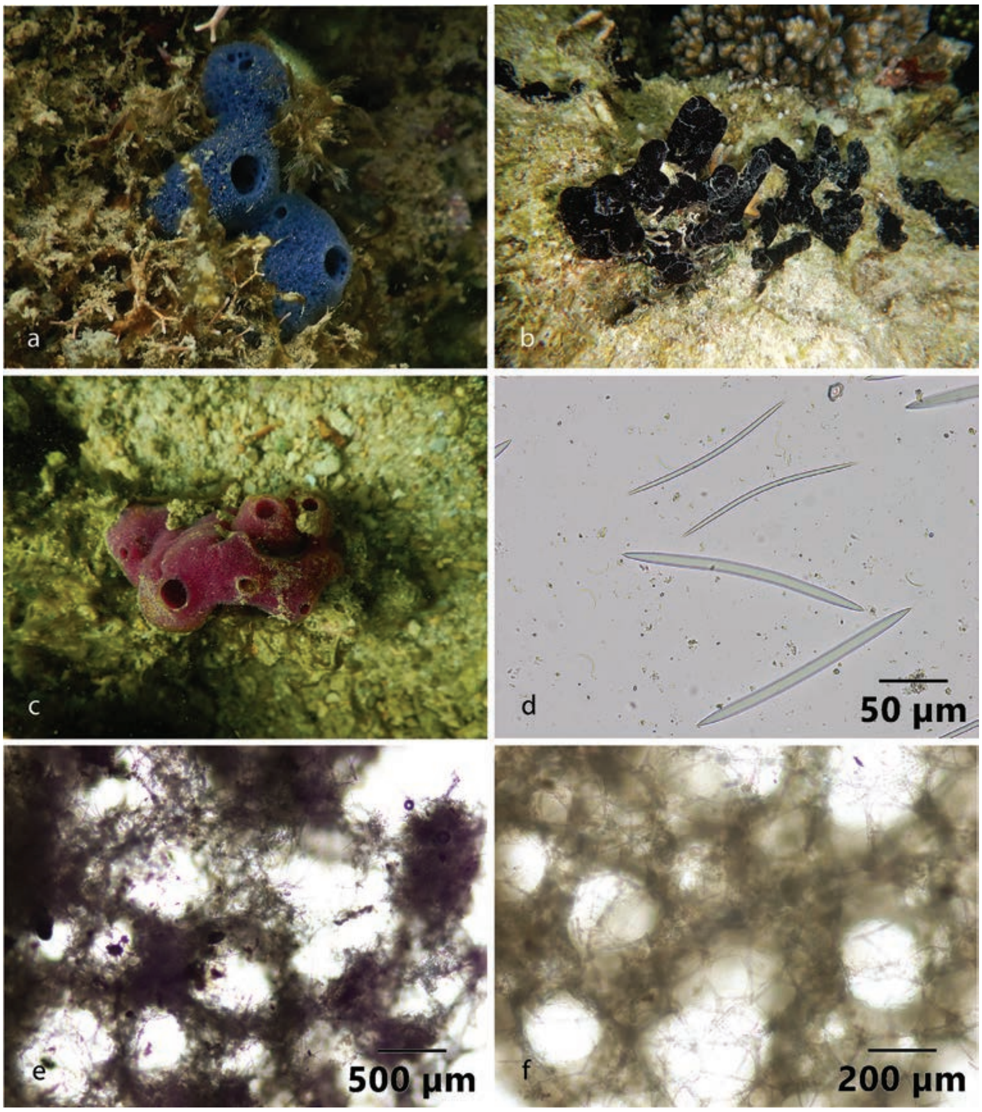


Figure 9. Habitus in situ **a** *Haliclona* (*Soestella*) *elegantia* (Bowerbank, 1875) at Kayangan Island, the Spermonde Archipelago **b** *Haliclona* (*Soestella*) sp. 1. at Samalona Island, the Spermonde Archipelago **c** *Haliclona* (*Soestella*) sp. 2. at Samalona Island, the Spermonde Archipelago (all photographs by SAP) **d** two sizes of oxeas and sigmas of *Haliclona* (*Soestella*) *elegantia* **e** *Haliclona* (*Soestella*) *elegantia* spicules reticulation **f** *Haliclona* (*Soestella*) sp. 2. spicule reticulation.

Haliclona (*Soestella*) sp. 2

Fig. 9c, f

Diagnostic features. Small specimen (l × w × h; 45 × 32 × 25 mm) with magenta color in life and pale white in alcohol. Massive shape with large osculum. Ectosomal skeleton shows multispicular fiber tracts. Spicules are oxeas, larger oxeas 102–130.9 (116.1) × 3.8–6.5 (5) µm (n = 24), and thin oxeas 78.4–114.4 (96.8) × 1.3–4.1 (2.5) µm (n = 20). Rounded meshes formed by the spicules characterized those species as belonging to the subgenus *Soestella* (de Weerdt 2000). However, due to differences in color and variation of the macro-morphology, it can be distinguished from *Haliclona* (*Soestella*) *elegantia*.

Distribution and ecology. West Kayangan Island and Gusung Tallang Island, the Spermonde Archipelago; turbid environment.

Family Niphatidae van Soest, 1980
Genus *Amphimedon* Duchassaing & Michelotti, 1864

Amphimedon paraviridis Fromont, 1993
Fig. 10

Diagnostic features. Encrusting and soft, with small oscula and scattered ostia on the surface. Pale green in life and turning brown in alcohol. Skeleton isotropic reticulation arranged by oxeas 155–194 (173.5) × 5.9–8.1 (7.2) µm. *Amphimedon paraviridis* has similarities with *Amphimedon viridis* Duchassaing & Michelotti, 1864 from the Caribbean Sea. However, the holotype of *A. paraviridis* (from the Great Barrier Reef) has thicker spicules, a much greater spongin component, thicker fibers, and larger mesh spaces compared to *A. viridis* (Fromont 1993). Only three species of *Amphimedon* have been reported from the marine ecoregions of Indonesia (Putra et al. 2023), including *Amphimedon anastomosa* Calcinai et al., 2017, *Amphimedon zamboangae* (Lévi, 1961), and *Amphimedon denhartogi* de Voogd, 2003.

Distribution and ecology. Previously reported from Australia (Fromont 1993). This is first record of *Amphimedon paraviridis* from Samalona Island, the Spermonde Archipelago. Reef flat, overgrowing another sponge, *Clathria* (*Thalysias*) *reinwardti* Vosmaer, 1880.

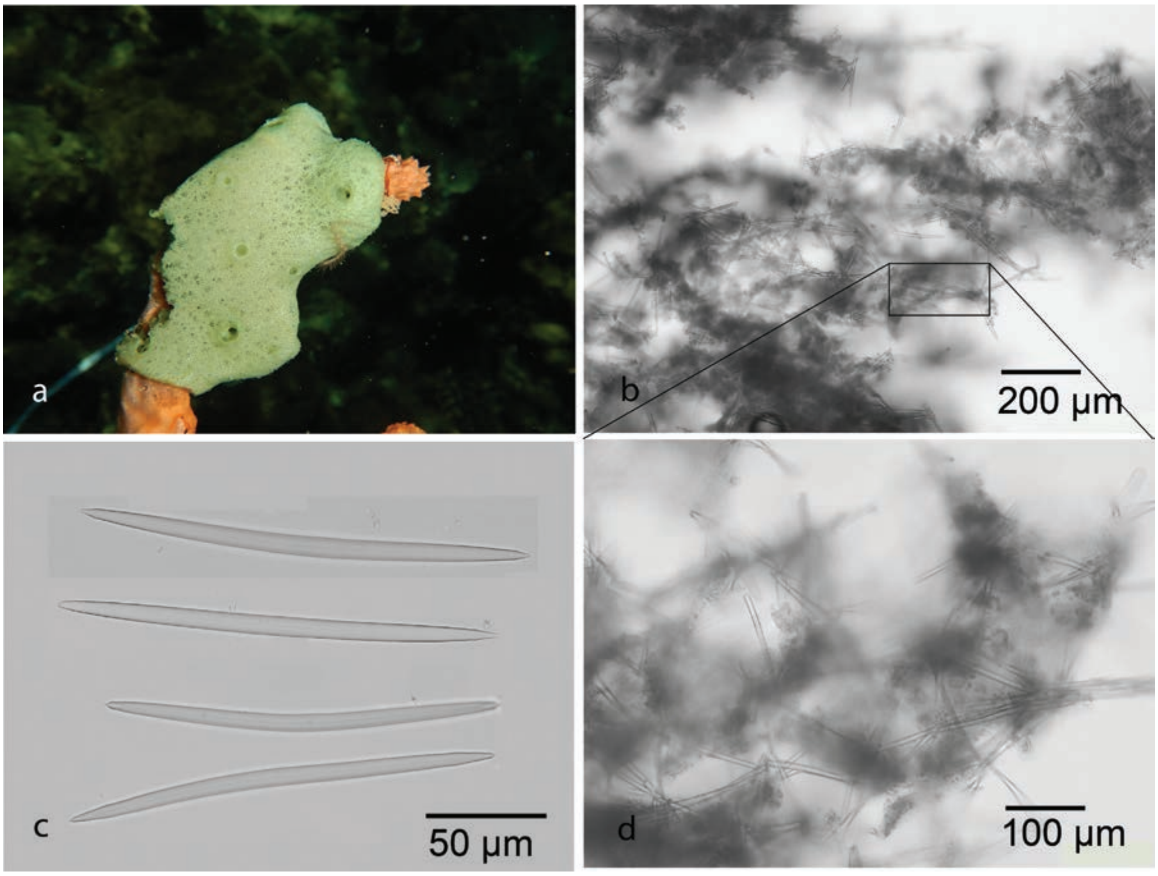


Figure 10. *Amphimedon paraviridis* Fromont, 1993 **a** habitus in situ over growing *Clathria* (*Thalysias*) *reinwardti* Vosmaer, 1880 at Samalona Island, the Spermonde Archipelago (photograph by SAP) **b** LM image of cross section of the skeleton **c** oxeas **d** Isotropic reticulation of oxeas.

Genus *Niphates* Duchassaing & Michelotti, 1864

Niphates nitida Fromont, 1993

Fig. 11

Diagnostic features. Ramose repent sponge. Bluish green in life, pale white in alcohol. Oscula are small, 2–4 mm in diameter. Ectosomal shows reticulation fiber tract. Oxeas slightly curved, larger oxeas 120.3–171.3 (139.4) × 4.8–9.3 (6.1) μm (n = 22), thin oxeas 109.3–132.7 (121) × 2.4–5.3 (3.5) μm (n = 14). Microscleres are C-shaped sigmas. This specimen is identified as *Niphates nitida* due to the reticulation fiber tract on the skeleton and the present of sigmas. Previously, only two species of *Niphates* recorded from Indonesia. *Niphates laminaris* Calcinai et al., 2017 is characterized by a non-spiny, rather irregular, microconulose surface and a chaonosomal skeleton with primary and secondary reticulation fiber tracts, as well as numerous microscleres (Calcinai et al. 2017). *Niphates olemda* (de Laubenfels, 1954) is a tubular sponge with small oxeas (de Laubenfels 1954). *Niphates nitida* is a new record for Indonesia.

Distribution and ecology. Previously was reported from Magnetic Island, Australia (Fromont 1993). This is first record for the Spermonde Archipelago (at Kayangan Island; turbid environment).

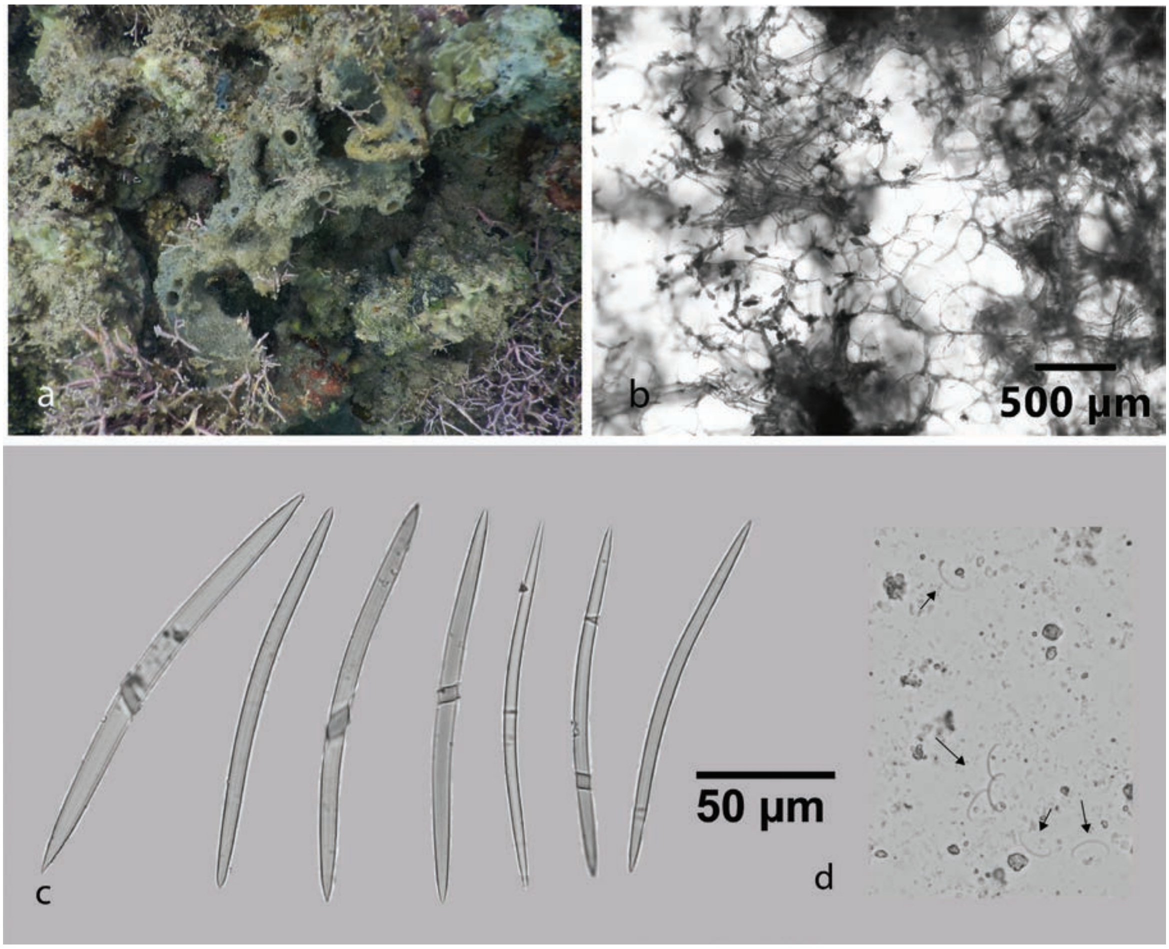


Figure 11. *Niphates nitida* Fromont, 1993 **a** habitus in situ at Kayangan Island, the Spermonde Archipelago (photograph by SAP) **b** ectosmal skeleton **c** oxeas **d** sigmas

Family Petrosiidae van Soest, 1980
Genus *Petrosia* Vosmaer, 1885
Subgenus *Petrosia* Vosmaer, 1885

Petrosia (*Petrosia*) *hoeksemai* de Voogd & van Soest, 2002
Fig. 12

Diagnostic features. The sponge is thick, massive, and encrusting with rugose surface. Color brown outside, cream inside, and turning blackish brown after preservation. Choanosomal skeleton shows pauci-multispicular spicule tracts. Three sizes of oxeas, primary oxeas 182.3–272.9 (219.6) × 10.8–19.2 (14.6) µm (*n* = 28), secondary oxeas 126.4–221.7 (173.6) × 6.7–11.4 (8.7) µm (*n* = 32), and tertiary oxeas 58–123.9 (83.1) × 5.6–10.5 (7.5) µm (*n* = 28).

Seven species of *Petrosia* have been reported from the Spermonde Archipelago, i.e., *Petrosia* (*Petrosia*) *hoeksemai* de Voogd & van Soest, 2002, *Petrosia* (*Petrosia*) *alfiani* de Voogd & van Soest, 2002, *Petrosia* (*Petrosia*) *lignosa* Wilson, 1925, *Petrosia* (*Petrosia*) *nigricans* Lindgren, 1897, *Petrosia* (*Petrosia*) *plana* Wilson, 1925, *Petrosia* (*Strongylophora*) *cortica* (Wilson, 1925),

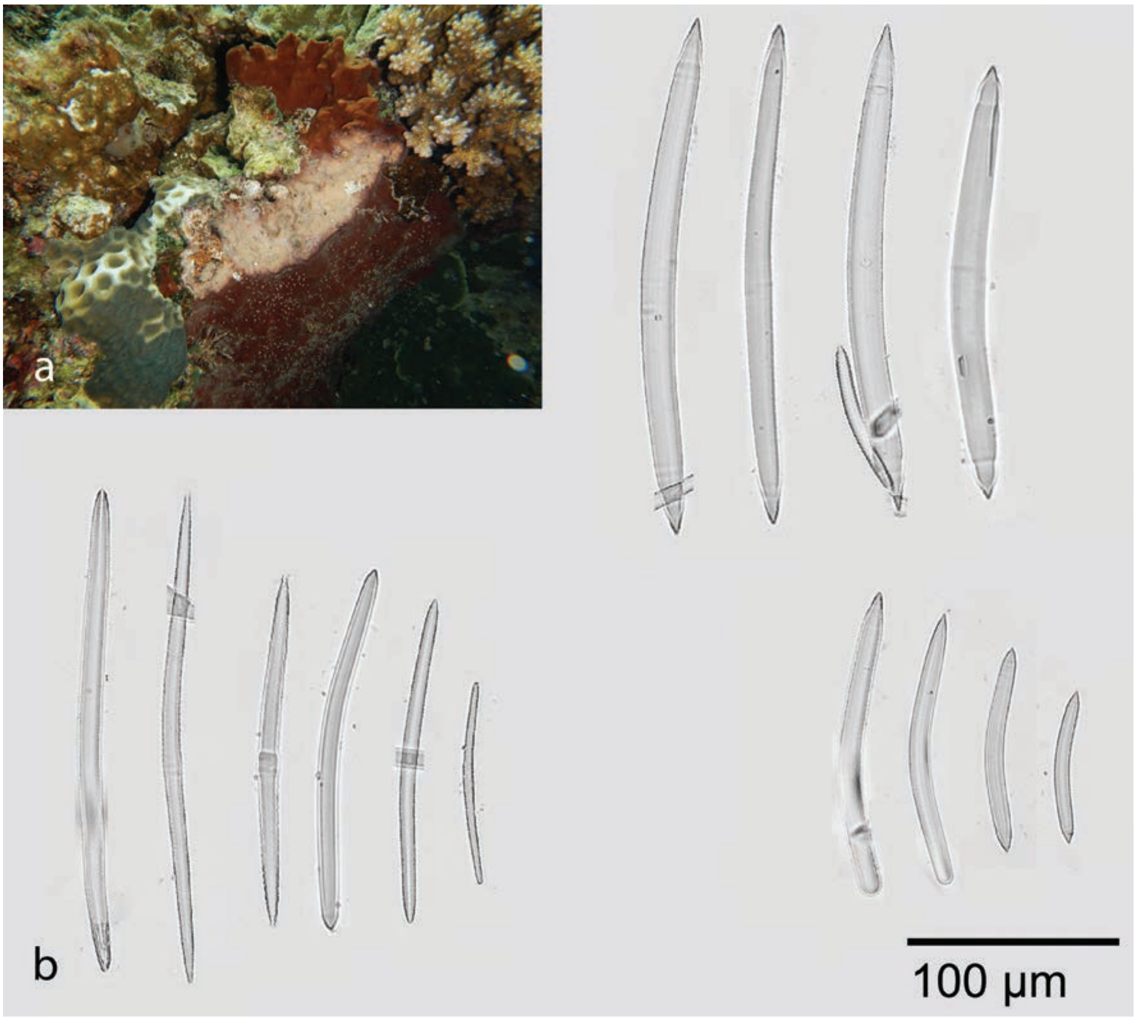


Figure 12. *Petrosia* (*Petrosia*) *hoeksemai* de Voogd & van Soest, 2002 **a** habitus in situ at Samalona Island, the Spermonde Archipelago (photograph by SAP) **b** three sizes of oxeas.

and *Petrosia* (*Strongylophora*) *strongylata* (Thiele, 1903). Two species were originally described from this area, *Petrosia* (*Petrosia*) *alfiani* and *Petrosia* (*Petrosia*) *hoeksemai* (de Voogd and van Soest 2002). Our specimen shows slightly bigger secondary and tertiary oxeas compare to the de Voogd & van Soest (2002) specimen. Comparison of spicules measurement between Indonesian *Petrosia* specimen are shown in Table 1.

Distribution and ecology. Samalona Island, the Spermonde Archipelago, attached vertically; reef flat; also reported from north Sulawesi (de Voogd and van Soest 2002).

Order Poecilosclerida Topsent, 1928
Family Coelosphaeridea Dendy, 1922
Genus *Lissodendoryx* Topsent, 1892
Subgenus *Waldoshmittia* de Laubenfels, 1936

Lissodendoryx (*Waldoschmittia*) *schmidti* (Ridley, 1884)
Fig. 13

Diagnostic features. Ectosome is formed of tangentially arranged tylotes and ascending bundles in a plumose arrangement. Main skeleton is an irregular reticulation of oxeas, with triangular meshes of spicules. Microscleres are isochelas and sigmas (Hofman and van Soest 1995).

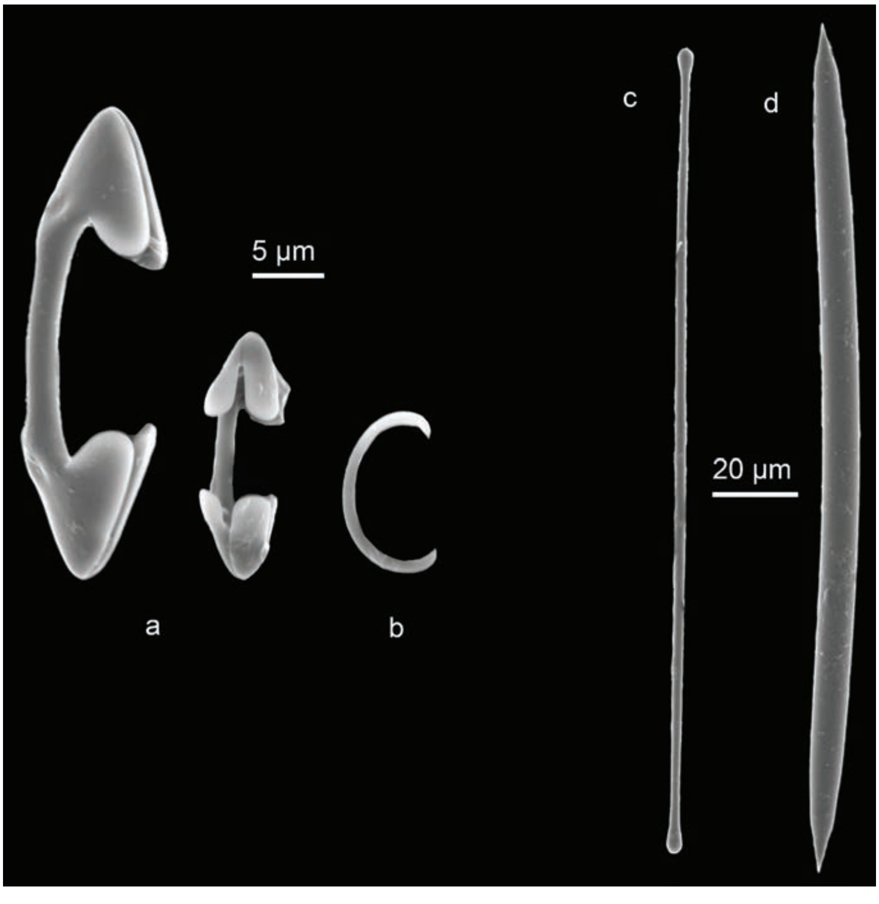


Figure 13. *Lissodendoryx* (*Waldoschmittia*) *schmidti* (Ridley, 1884) (CEL079) **a** SEM images of isochelae **b** sigma **c** tylote **d** oxea.

Distribution and ecology. This species also known from mesophotic zone. Previously recorded from Cochin-China, East Africa, Hawaii, Red Sea, Seychelles, and South Australia. In parts of Indonesia it was recorded from Ternate, Banda Sea, Aru Island (Arafura Sea), Flores, Jedan Island, East Java, and Sumba (Hofman and van Soest 1995). Our specimen is the first record for the Spermonde Archipelago, Lumulumu Island; reef flat.

Family Iotrochotidae Dendy, 1922
Genus *Iotrochota* Ridley, 1884

Iotrochota baculifera Ridley, 1884
Fig. 14

Diagnostic features. Black, thin, encrusting with rough surface, and boring. Choanosomal skeleton show multispicular reticulation. Spicule arrangements are styles 157.9–212.5 (191.7) × 7.4–15.9 (11.4) µm (*n* = 25), strongyles 248–287.6 (266.6) × 3.6–7.8 (6.7) µm (*n* = 25), with microsclere birotulate chelae, 13.9–17.3 (15.4) µm (*n* = 21). *Iotrochota baculifera* has similar coloration with *Iotrochota purpurea* (Bowerbank, 1875) and *Iotrochota nigra* (Baer, 1906). Table 2 shows the comparison of the spicule measurements of these species.

Distribution and ecology. Widespread from the Western Indian Ocean to Hawaii (Núñez Pons et al. 2017). Only two species of *Iotrochota* have been recorded from Spermonde Archipelago, *Iotrochota purpurea* and *Iotrochota baculifera*

Table 1. Comparison of spicule measurements (µm) in specimens of *Petrosia* (*Petrosia*) and *Petrosia* (*Strongylophora*) from Indonesia.

Species	Oxeas/ Strongyles 1	Oxeas/ Strongyles 2	Oxeas/ Strongyles 3	Reference
Petrosia (*Petrosia*) *hoeksemai*	182.3–272.9 × 10.8–19.2	126.4–221.7 × 6.7–11.4	58–123.9 × 5.6–10.5	This study
Petrosia (*Petrosia*) *hoeksemai*	240–305 × 10–20	90–130 × 7–12	40–75 × 5–9	(de Voogd and van Soest 2002)
Petrosia (*Petrosia*) *alfiani*	183–253 × 10–15	106–153 × 7–14	60–70 × 6–7	(de Voogd and van Soest 2002)
Petrosia (*Petrosia*) *lignosa*	230–300 × 14–18	75–150 × 10–13	35–65 × 7–10	(de Voogd and van Soest 2002)
Petrosia (*Petrosia*) *nigricans*	240–305 × 8–16	120–188 × 9–10	57–85 × 5	(de Voogd and van Soest 2002)
Petrosia (*Petrosia*) *plana*	190–290 × 7–14	95–130 × 7–9.5	43–75 × 5–9	(de Voogd and van Soest 2002)
Petrosia (*Strongylophora*) *cortica*	300–360 × 11–14	80–200 × 11–14	21–50 × 3–9	(de Voogd and van Soest 2002)
Petrosia (*Strongylophora*) *strongylata*	326 × 18	95–145 × 10–12	44–60 × 8–12	(de Voogd and van Soest 2002)

Table 2. Comparison of spicule measurements (µm) in specimens of *Iotrochota baculifera*, *Iotrochota purpurea*, and *Iotrochota nigra*.

Species	Styles	Strongyles	Birotulates	Reference
Iotrochota baculifera	157.9–212.5 (191.7) × 7.4–15.9 (11.4)	248–287.6 (266.6) × 3.6–7.8 (6.7)	13.9–17.3	This study
Iotrochota baculifera	200 × 9.5–12.7	220–280 × 6.3	16	(Ridley 1884)
Iotrochota baculifera	125–180 × 5.5–7.5	225–255 × 3.5–5	13–16.5	(Bergquist 1965)
Iotrochota baculifera	168–189 (175) × 4–8 (6)	201–243 (225) × 4–6 (4)	12	(Thomas 1973)
Iotrochota baculifera	145–170 (160) × 5–8.7 (7.5)	205–230 (220.9) × 2.5–5 (4)	12	(Núñez Pons et al. 2017)
Iotrochota purpurea	146–180(163) × 4–8(5)	-	16	(Thomas 1973)
Iotrochota purpurea	168 × 8	-	-	(Thomas 1991)
Iotrochota nigra	170 × 6	-	-	(Baer 1906)
Iotrochota nigra	230–269 (251) × 5 (5)	163–193(184) × 7(7)	17(17)	(Samaai et al. 2019)

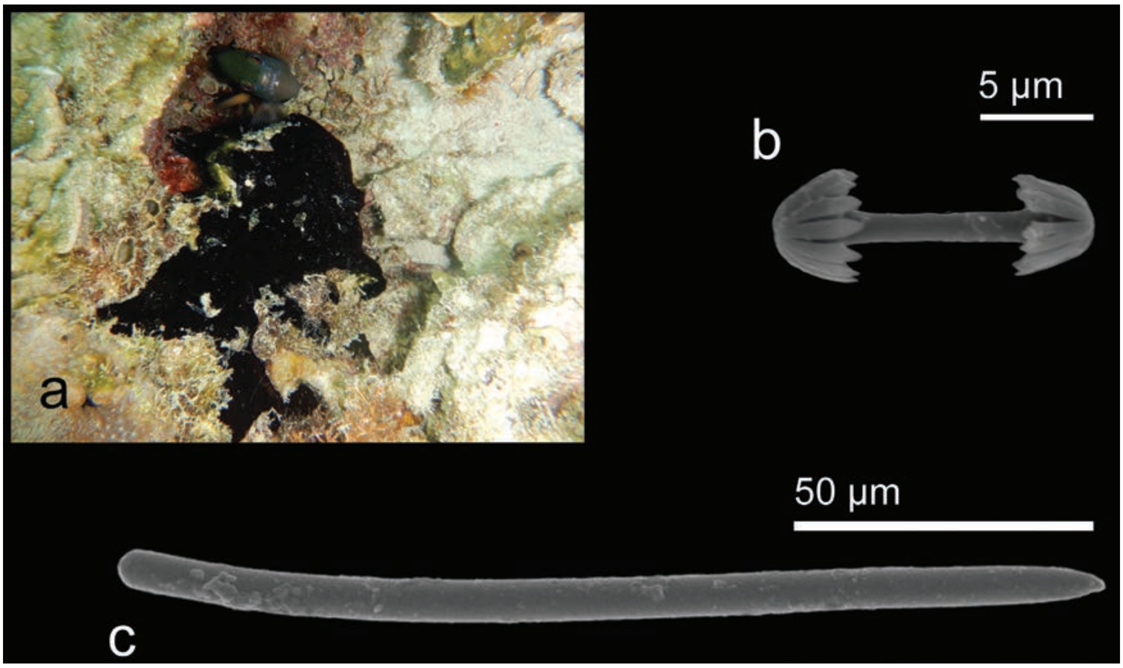


Figure 14. *Iotrochota baculifera* Ridley, 1884 **a** habitus in situ at Samalona Island, the Spermonde Archipelago (photograph by SAP) **b** birotulate chelae **c** styles.

Ridley, 1884 (de Voogd 2005). Our specimen was found in the north-west of Samalona Island, the Spermonde Archipelago; reef flat.

Family Microcionidae Carter, 1875
Genus *Clathria* Schmidt, 1862
Subgenus *Thalysias* Duchassaing & Michelotti, 1864

Clathria (*Thalysias*) *reinwardti* Vosmaer, 1880
Fig. 15

Diagnostic features. Arborescent, simple massive, and very repent appearance with many small oscula. Bright to dark orange in living material, and brown in alcohol. Reticulate skeleton with two class sizes of styles and echinating acanthostyles. Principal styles slightly curved with strongylote point, 151–312 (205.5) × 5.3–10.85 (7.4) µm (*n* = 28), auxiliary styles straight and slightly curved, 72–163 (106.5) × 1.5–4.7 (3.4) µm (*n* = 37), and echinating acanthostyles with short, rounded point and dense spines on point and base, 51.9–81.5 (67.1) × 6.2–8.7 (7.3) µm (*n* = 31). This species can be differentiated from other similar *Thalysias* by its characteristic acanthostyle morphology, growth form, and the size and geometry of its toxas, including ectosomal-subectosomal features (Hooper 1996). Hooper's (1996) specimen shows microscleres as palmate isochelae in two size classes and oxhorn toxas.

Distribution and ecology. Central Indian Ocean (Thomas 1986), Indo-Pacific (van Soest 1990; Lim et al. 2016), and Australia (Hooper 1996). Commonly found in coral rubble or dead coral and hard substrates. Our specimen was found in the Spermonde Archipelago, the north-west of Samalona Island; reef flat and Gusung Tallang; turbid reef.

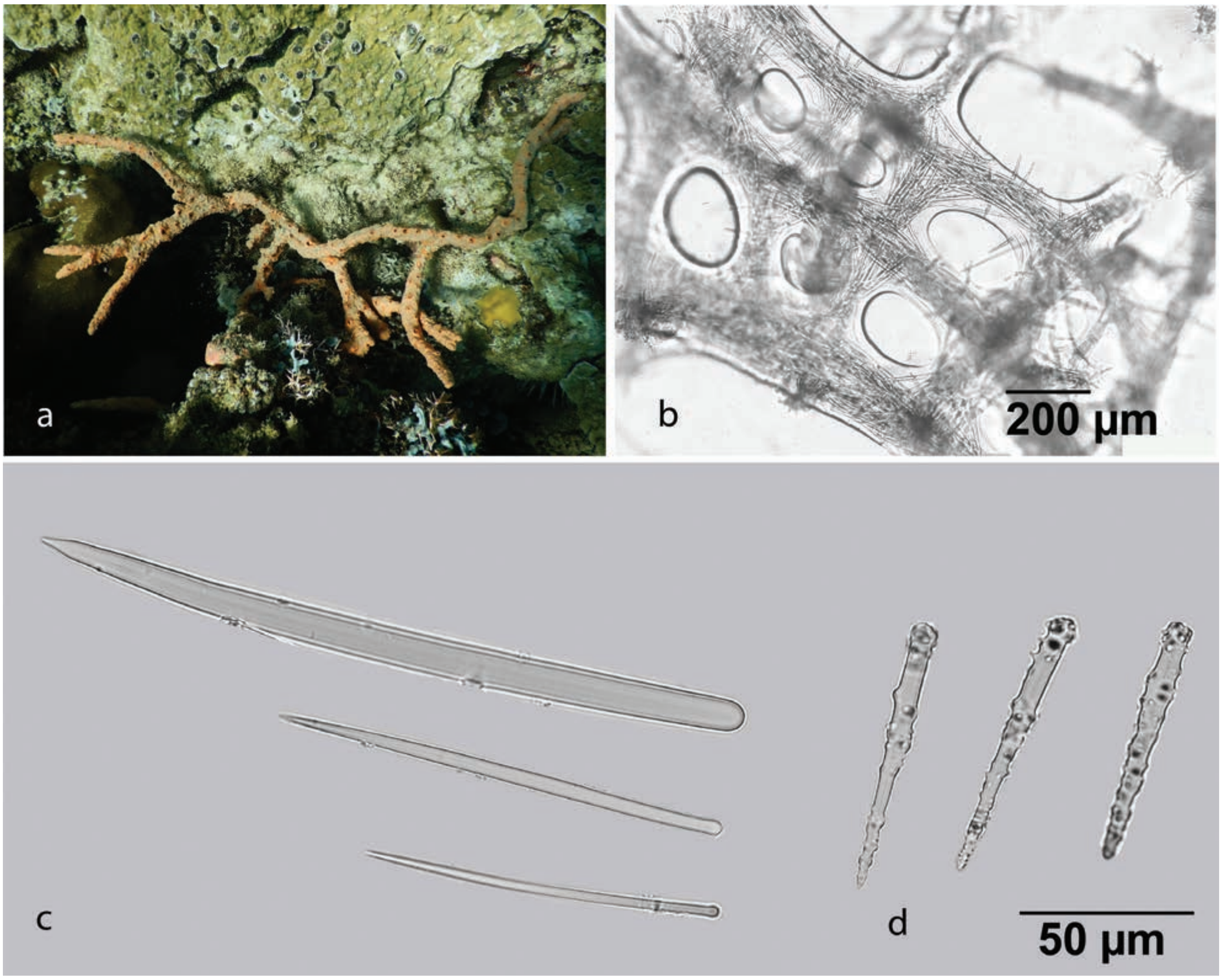


Figure 15. *Clathria* (*Thalysias*) *reinwardti* Vosmaer, 1880 **a** habitus in situ at Samalona Island, the Spermonde Archipelago (photograph by SAP) **b** longitudinal section of the skeleton **c** styles **d** acanthostyles.

Order Scopalinida Morrow & Cárdenas, 2015
Family Scopalinidae Morrow et al., 2012
Genus *Stylissa* Hallmann, 1914

Stylissa massa (Carter, 1887)
Fig. 16

Diagnostic features. Massive, soft, and friable with rough surface and medium-sized oscula appear on top of the ridge. Yellow-orange in life and brown in alcohol. Spicules arrangements are of styles and strongyles.

Distribution and ecology. *Stylissa massa* is widely distributed in the Indo-Pacific (Erpenbeck et al. 2017). Since *Stylissa massa* is known to be widespread, and recent studies using molecular techniques show the probability of distinct cryptic lineages of this species in the Indo-Pacific (Erpenbeck et al. 2017). Our specimen was collected from the Spermonde Archipelago, south-west of Samalona Island; reef flat, attached to rubble and dead coral skeletons.

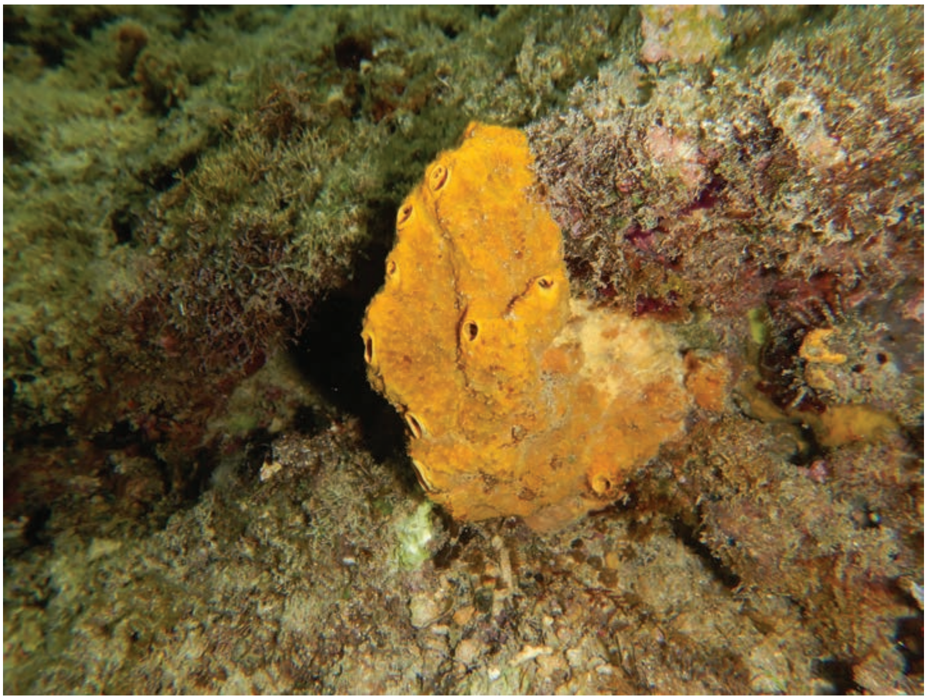


Figure 16. Habitus in situ of *Stylissa massa* (Carter, 1887) at Samalona Island, the Spermonde Archipelago (photograph by SAP).

Order Suberitida Chombard & Boury-Esnault, 1999
Family Halichondriidae Gray, 1867
Genus *Halichondria* Fleming, 1828
Subgenus *Halichondria* Fleming, 1828

Halichondria (*Halichondria*) *cartilaginea* (Esper, 1797)
Fig. 17

Description. Massive creeping growth form with upright branches (branching). These branches are irregular and form mats covering the substrate. Color bright green, flexible/cartilaginous. This species lives in association with Chlorophyta *Cladophoropsis vaucheriiformis* (Areschoug) Papenfuss, 1958 (van Soest 1990). Spicules are only oxeas, 125.46–252.45 (191.40) × 4.03–7.40 (5.37) µm.

Distribution and ecology. Currently this species is recorded from China, Vietnam, Malacca Strait, Banda Sea, and East African Coral Coast. According to the WPD checklist (de Voogd et al. 2024), this is the first record from the Spermonde Archipelago, Badi Island; reef flat.

Genus *Topsentia* Berg, 1899

Topsentia indica Hentschel, 1912
Fig. 18

Description. Only two species of *Topsentia* are distributed in Indonesia, i.e., *Topsentia dura* (Lindgren, 1897) and *Topsentia indica* Hentschel, 1912. *Topsentia dura* had further illustrations and spicule measurements provided

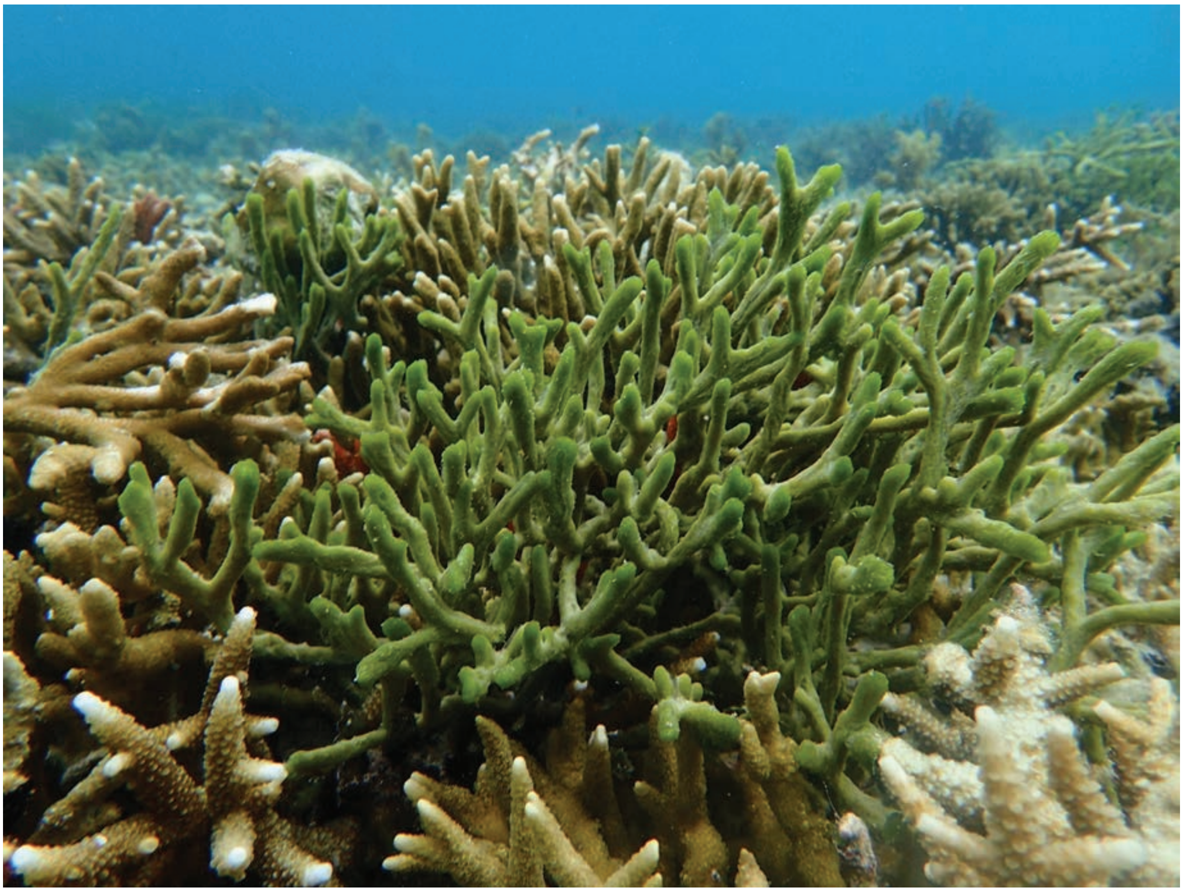


Figure 17. Habitus in situ of *Halichondria* (*Halichondria*) *cartilaginea* (Esper, 1797) (CEL025) (photograph by NJdeV).

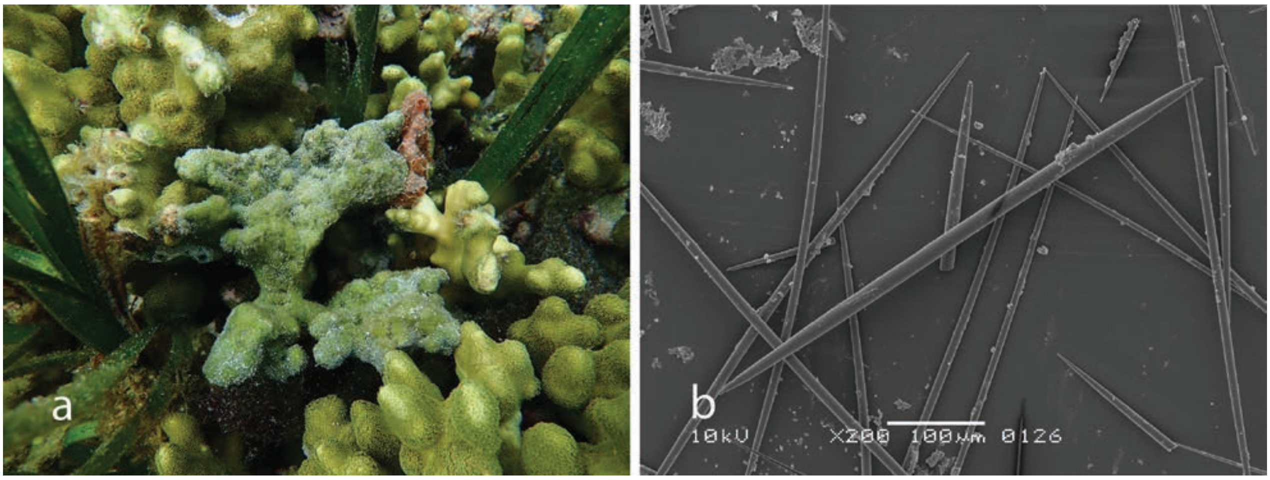


Figure 18. *Topsentia indica* Hentschel, 1912 **a** habitus in situ at Langkai Island, the Spermonde Archipelago (photograph by NJdeV) **b** SEM images of the spicules.

by a previous study (Alvarez and Hooper 2011). These species are massive, of hard consistency with skeletons made of a confused mass of oxeas of similar dimensions, not clearly differentiated into size classes. Our specimen shows similar characteristics with the specimen of Hentschel (1912).

Distribution and ecology. Previously recorded from Aru Islands (Hentschel 1912). This is first record from the Spermonde Archipelago, Langkai Island; reef flat.

Family Suberitidae Schmidt, 1870
Genus *Suberites* Nardo, 1833

Suberites sp.
Fig. 19

Diagnostic features. Ficiform (fig-shaped) with orange (almost red) color and fragile. Oscula found on top of the fig-like shape. Aquiferous network can be seen from ectosomal skeleton of living specimen, small ostia also visible. Spicules are tylostyles (total length × width) 204.3–324.5 (278.4) × 3.5–8.6 (5.5) µm (*n* = 31). Tylostyle heads are oval with an indistinct neck (head length × head width × neck width) 8.8–15.9 (12.3) × 4.2–8.8 (6) × 3.2–8 (4.5) µm (*n* = 25).

Distribution and ecology. Only three *Suberites* species have been recorded from Indonesia, *Suberites radiatus* Kieschnick, 1896, *Suberites diversicolor* Becking & Lim, 2009, and the deep-sea *Suberites perfectus* Ridley & Dendy, 1886 (Becking and Lim 2009; Putra et al. 2023). North-west of Samalona Island, the Spermonde Archipelago; reef flat, scattered across shallow water area, growth on rock, plastic PVC, and sometimes competing with Scleractinia.

Figure 19. Habitus in situ of *Suberites* sp. (photograph by SAP).

Genus *Terpios* Duchassaing & Michelotti, 1864

Terpios hoshinota **Rützler & Muzik, 1993**
Fig. 20

Diagnostic features. Thin (< 1 mm thick), encrusting, and excavating form overgrowing host coral skeletons (*Acropora* spp.). Dark grey to black, sometime pale grey in the upper surface. Original description of *Terpios hoshinota* show spicules as only tylostyles (Rützler and Muzik 1993). In this study, spicule arrangements are tylostyles (total length × width) 132.9–252 (206.9) × 2.6–7.8 (4.4) μm (*n* = 52), and variation of heads (head length × head width × neck width) 3.7–7.4 (5.4) × 4.8–9 (6.5) × 1.8–5 (3.3) μm (*n* = 27). Spicule dimension measurements are shown on Table 3. The morphology of *Terpios hoshinota* is similar to *Terpios granulosus* Bergquist, 1967 from Hawaiian reefs. The difference is that this species is greyish brown, has lobe-headed tylostyles, and has a cyanobacterial symbiont (Rützler and Muzik 1993). This species known as a coral-killing sponge, but a recent study shows *Terpios hoshinota* could also grow on glass slides, plastic sheets, and rubber tyres. The competitive interaction with the coral host is only for substrate rather than food or nutrients (Syue et al. 2021).

Distribution and ecology. This widespread species has been recorded from the Indian Ocean, north-western Pacific, and Australia (Fromont et al. 2019).

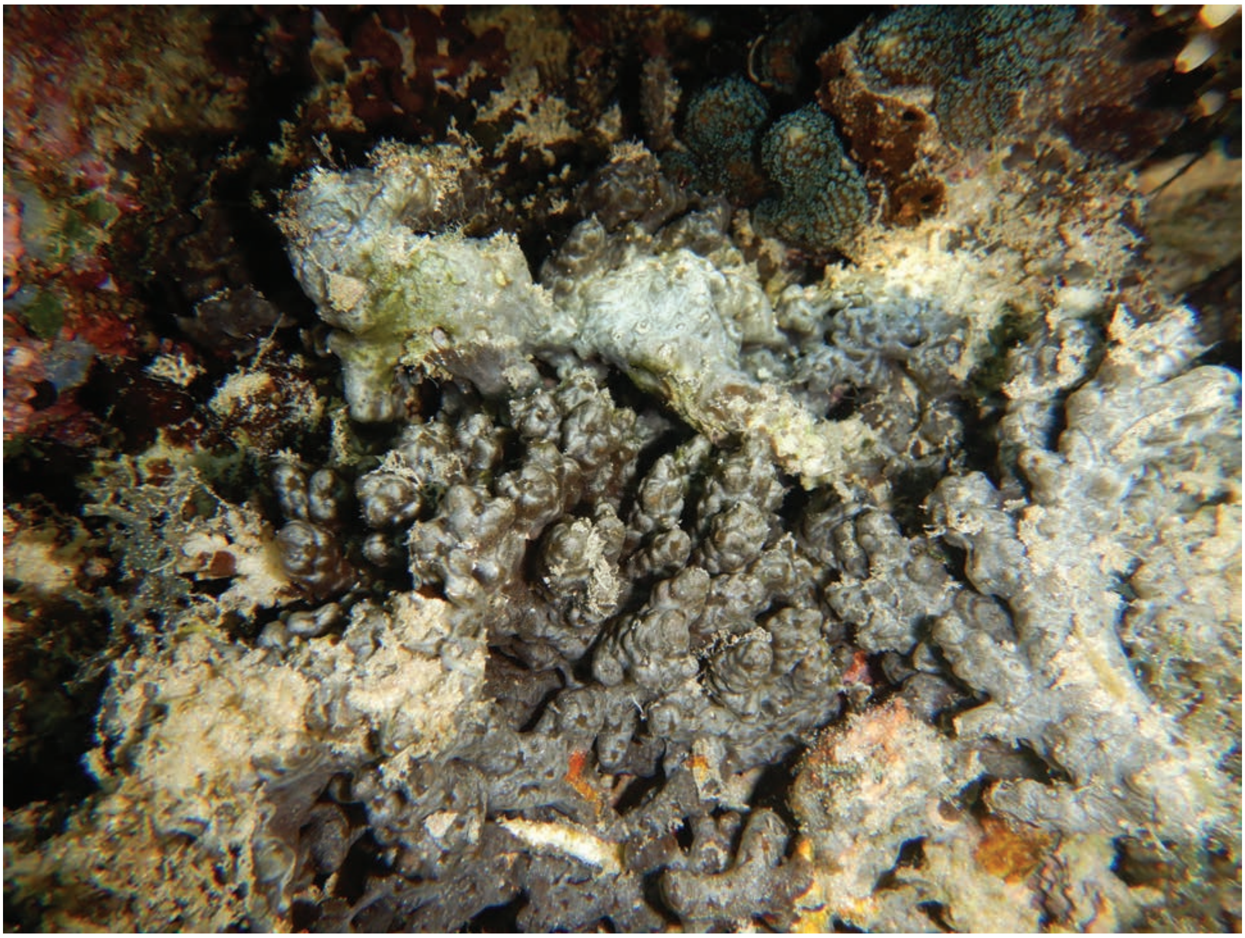


Figure 20. Habitus in situ of *Terpios hoshinota* Rützler & Muzik, 1993 (photograph by SAP).

Table 3. Spicule (tylostyles) dimensions (μm) for *Terpios hoshinota*.

Total length	Shaft width	Neck width	Head width	Head length	Reference
132.9–252 (206.9)	2.6–7.8 (4.4)	1.8–5 (3.3)	4.8–9 (6.5)	3.7–7.4 (5.4)	This study
180–290 (251.6)	3–4 (3.5)	2–3 (2.7)	5.5–7 (6.1)	4.5–6 (5.2)	(Rützler and Muzik 1993)

Terpios hoshinota was originally described from the Ryukyu Archipelago, Japan (north-west Pacific). Our specimen was found from north-west of Samalona Island, the Spermonde Archipelago; reef flat, overgrowing branching *Acropora* sp.

Order Tetractinellida Marshall, 1876
Family Ancorinidae Schmidt, 1870
Genus *Ecionemia* Bowerbank, 1862

Ecionemia acervus Bowerbank, 1862
Fig. 21

Description. Massive or thickly encrusting sponges without a distinct cortex. Megascleres are triaenes of different types and large oxeas. Microscleres in-

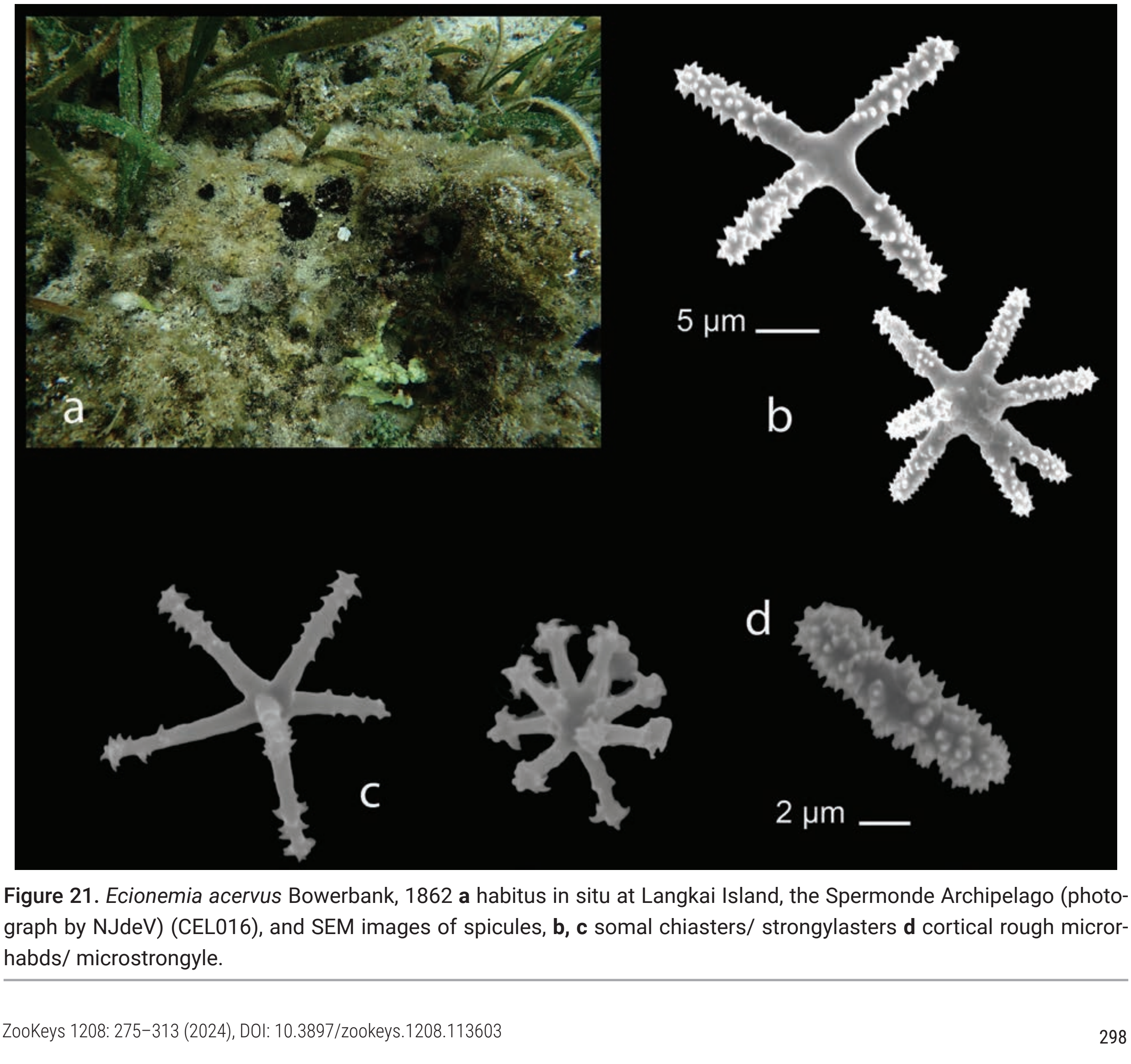


Figure 21. *Ecionemia acervus* Bowerbank, 1862 **a** habitus in situ at Langkai Island, the Spermonde Archipelago (photograph by NJdeV) (CEL016), and SEM images of spicules, **b, c** somal chiasters/ strongylasters **d** cortical rough microrhabds/ microstrongyle.

clude spiny microrhabds in addition to euasters. Microrhabds usually form a dermal layer (Uriz 2002).

Distribution and ecology. Indo-Pacific, Australia, New Zealand. This species is common in the Indo-Pacific (Uriz 2002). Our specimen was collected from Langkai Island, the Spermonde Archipelago; reef flat.

Family Geodiidae Gray, 1867
Genus *Geodia* Lamarck, 1815

Geodia sp.

Fig. 22

Diagnostic features. Twelve species of *Geodia* spp. were described from Indonesia (Putra et al. 2023; de Voogd et al. 2024). Our specimen has oxeas 1079.43–1820.54 (1507.20) × 18.17–33.67 (25.21) µm (*n* = 11), sterrasters widths 49.05–77.40 (59.98) µm (*n* = 20), dichotriaene, anatriaene, protriaene, strongylasters, and oxyasters. Further analysis is needed to examine and provide a name for this specimen.

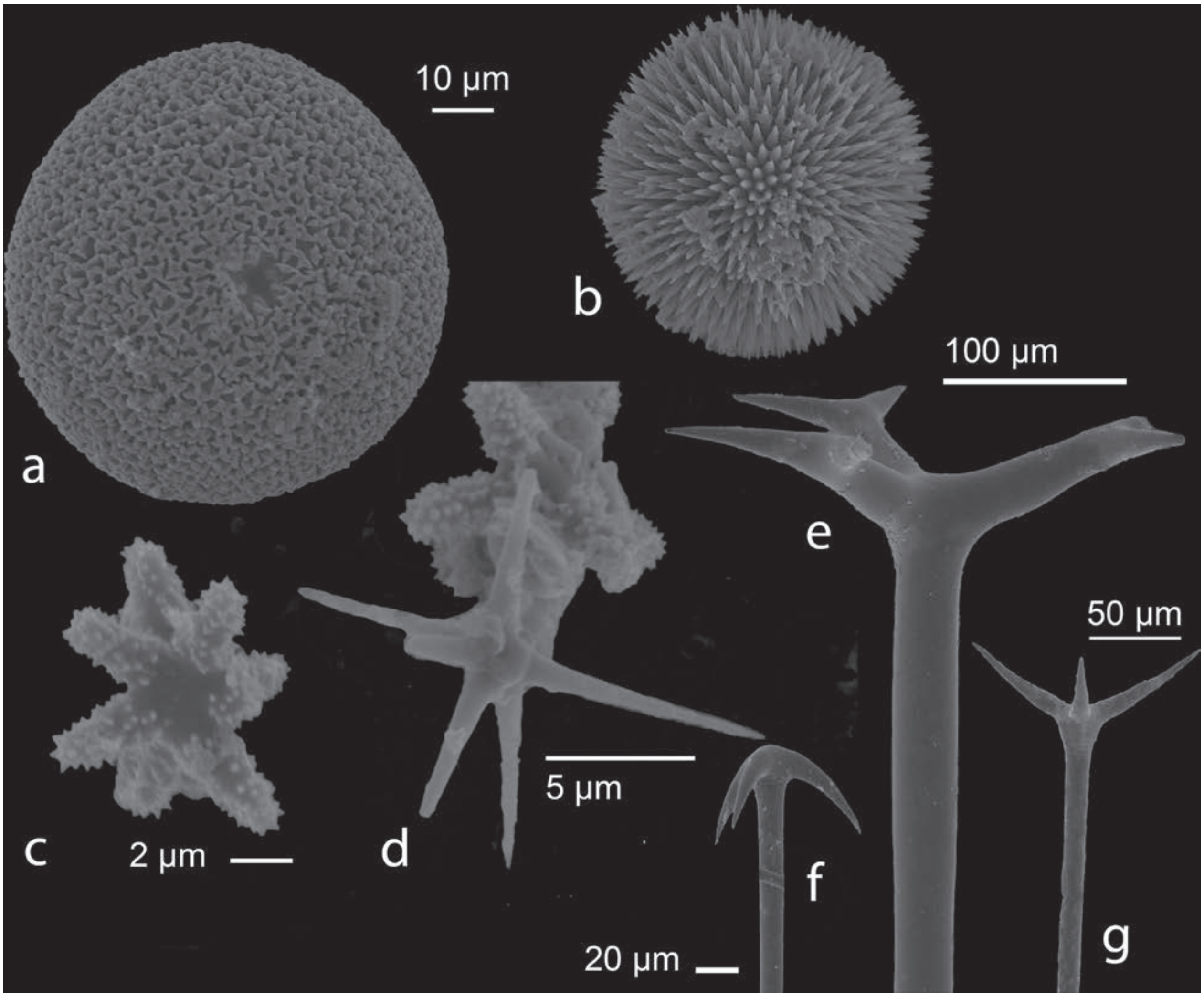


Figure 22. SEM images of spicules of *Geodia* sp. (CEL174) **a, b** sterrasters (**b** developmental stage) **c** strongylaster **d** oxyaster attached to strongylasters **e** dichotriaene **f** anatriaene **g** protriaene.

Distribution and ecology. This group is distributed across Indonesia, i.e., Halmahera, Arafura Sea, Southern Java, Sunda Shelf/Java Sea, Banda Sea, Palawan/North Borneo (Sollas 1888; Kieschnick 1896; Topsent 1897; Lindgren 1898; Thiele 1900; von Lendenfeld 1903; Hentschel 1912; Wilson 1925; van Soest et al. 2020). Our specimen was collected from Barangbaringan Island, the Spermonde Archipelago; turbid environment.

Family Tetillidae Sollas, 1886
Genus *Paratetilla* Dendy, 1905

Paratetilla bacca (Selenka, 1867)
Fig. 23

Diagnostic features. Globular sponges, specimen ≈ 64 × 47 mm (l × w) in diameter. Porocalices are abundant as circular to oval apertures. Color generally bright yellow when alive with brownish appearance in situ due to algal and sediment cover. Skeleton composed of oxea and triaenes radiating from a central core. Megascleres are oxeas, anatriaenes, and calthrops-like. Microscleres are sigmaspires, C- to S-shaped. A complete redescription of *P. bacca* was provided recently (Santodomingo and Becking 2018). This species had a considerable variation in spicules sizes in the different localities as well as significant intra-specific variation. This variation could be a response to different environmental conditions, a consequence of genetic selection, or synergistic between ecological and genetic factors.

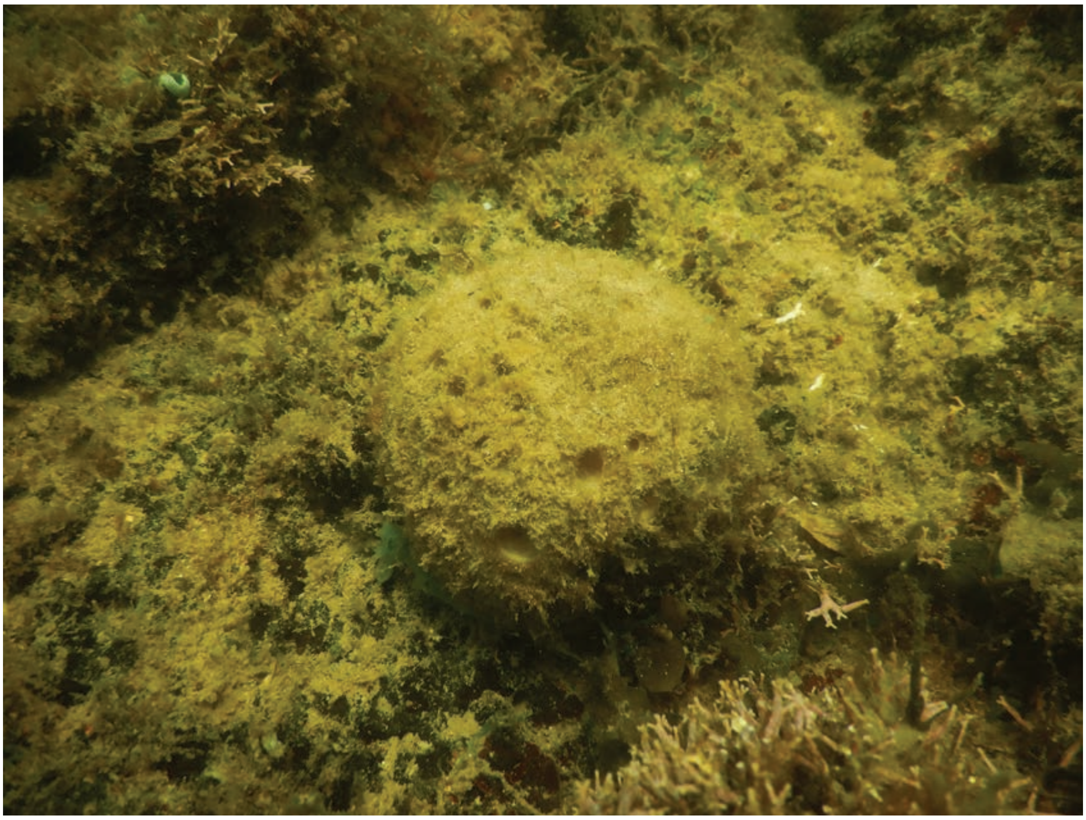


Figure 23. Habitus in situ of *Paratetilla bacca* (Selenka, 1867) at Gusung Tallang, the Spermonde Archipelago (photograph by SAP).

Distribution and ecology. Seychelles Islands (Thomas 1973), south-west Madagascar (Vacelet et al. 1976), Zanzibar (Pulitzer-Finali 1993), Thailand (Putchakarn 2007), Singapore (Lim et al. 2012), Philippines (Longakit et al. 2005), and Indonesia (Santodomingo and Becking 2018). Our specimen was collected from Gusung Tallang Island, the Spermonde Archipelago; turbid environment.

Subclass Keratosa Grant, 1861
Order Dictyoceratida Minchin, 1900
Family Dysideidae Gray, 1867
Genus *Lamellodysidea* Cook & Bergquist, 2002

Lamellodysidea herbacea (Keller, 1889)
Fig. 24

Diagnostic features. Live specimen found was white to pale green in color, and grey after preservation. This species habitus is soft, fragile, slick, thin (< 1 cm thick), and has an encrusting basal plate with a complex labyrinthine wall-like pattern. Skeleton structure forming interconnected reticulate fibers with several adjacent spicules. Various of microsymbionts (cyanobacteria) are found inhabiting it. Currently there only two species of *Lamellodysidea*, *Lamellodysidea herbacea* (Keller, 1889) and *Lamellodysidea chlorea* (de Laubenfels, 1954), both confused with each other. *Lamellodysidea herbacea* is known to be com-

Figure 24. Habitus in situ of *Lamellodysidea herbacea* (Keller, 1889) at Samalona Island, the Spermonde Archipelago (photograph by SAP).

mon in the sub-intertidal zone of the coral reef, which is exposed to sunlight (Putchakarn 2007). Molecular analysis shows *Lamellodysidea herbacea* is a diverse group and consists of several distinct lineages of the alleged single species, and has probably been misidentified in the past with undescribed lineages due to superficial resemblances (Erpenbeck et al. 2012).

Distribution and ecology. Our specimen was collected from Samalona Island, the Spermonde Archipelago; reef flat. This species was previously recorded from the Red Sea (Row 1911), India (George et al. 2020), Thailand (Putchakarn 2007), the Spermonde Archipelago (de Voogd et al. 2006), and the Great Barrier Reef (Hooper 2008).

Family Irciniidae Gray, 1867

Genus *Ircinia* Nardo, 1833

Ircinia schulzei (Dendy, 1905)

Fig. 25

Diagnostic features. Specimen attached to hard substrate, cylindrical with irregular short or club-shaped branches and rugose surface. Color in life is pale green and pale white in alcohol. Small oscula are found in every branch, sometimes on the tip. Skeleton is laminated fiber. Irciniidae are massive, or occasionally encrusting, sponges that display a wide range of forms, e.g., caliculate, lamelliform, lobate, and digitate. The species of *Ircinia* are pithed and laminated with primary and secondary fibers (de C. Cook and Bergquist 1999).

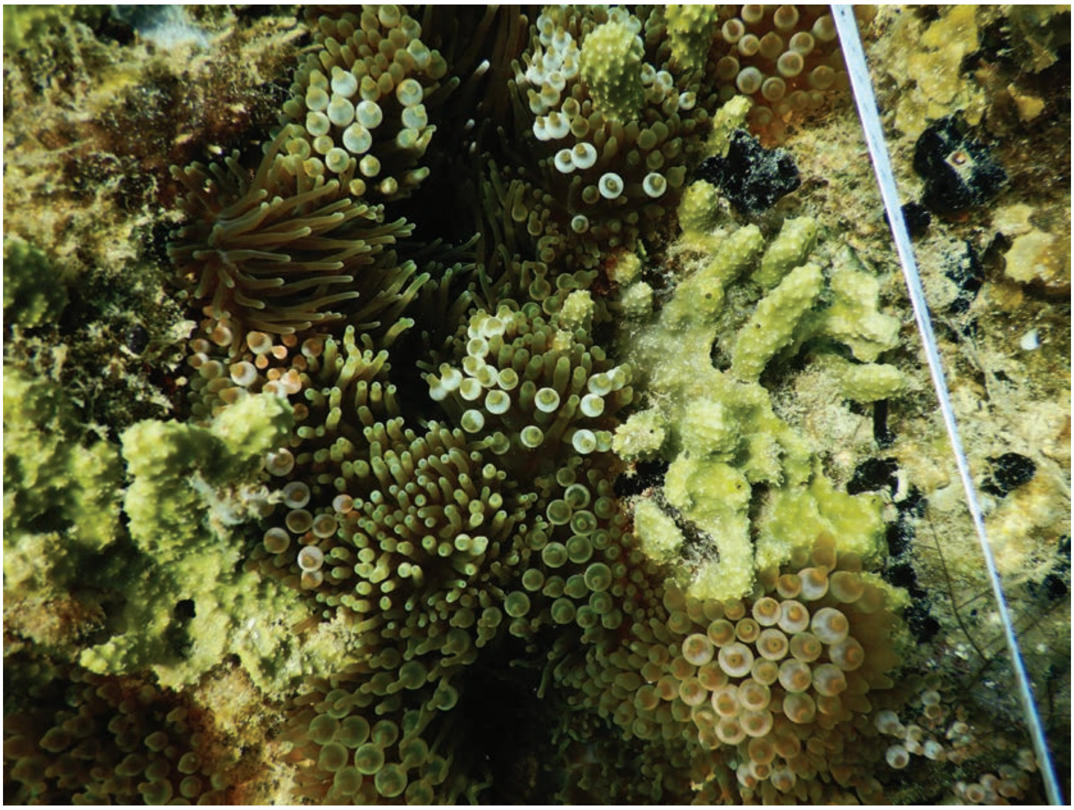


Figure 25. Habitus in situ of *Ircinia schulzei* (Dendy, 1905) at Samalona Island, the Spermonde Archipelago (photograph by SAP).

Distribution and ecology. *Ircinia schulzei* was first described from Ceylon (Sri Lanka today; Dendy 1905). A previous record from Papua New Guinea (Pulitzer-Finali and Pronzato 1999) and this new record in the Spermonde Archipelago shows that the species could be widespread in the Indo-Pacific region. Our specimen was found living between an anemone and other sponges on top of a rock in the reef flat of north-west of Samalona Island, the Spermonde Archipelago.

Family Thorectidae Bergquist, 1978

Genus *Phyllospongia* Ehlers, 1870

Phyllospongia foliascens (Pallas, 1766)

Fig. 26

Diagnostic features. Specimen form is foliaceous and irregular flabellate branches, pale white color in life and when preserved, < 0.5 mm thick. Numerous small oscula (< 1 mm) scattered in the surface. Skeleton consists of interconnected reticulate fibers. This species was recently transferred from the genus *Carteriospongia* Hyatt, 1877 due to molecular phylogenetic analysis showing *Carteriospongia foliascens* as a clade member of *Phyllospongia bergquistae* Abdul Wahab & Fromont, 2020. The original diagnosis describing a verrucose surface is characteristic for *Phyllospongia foliascens*, but with a fine and meandering surface patterning for *Phyllospongia bergquistae* (Bergquist et

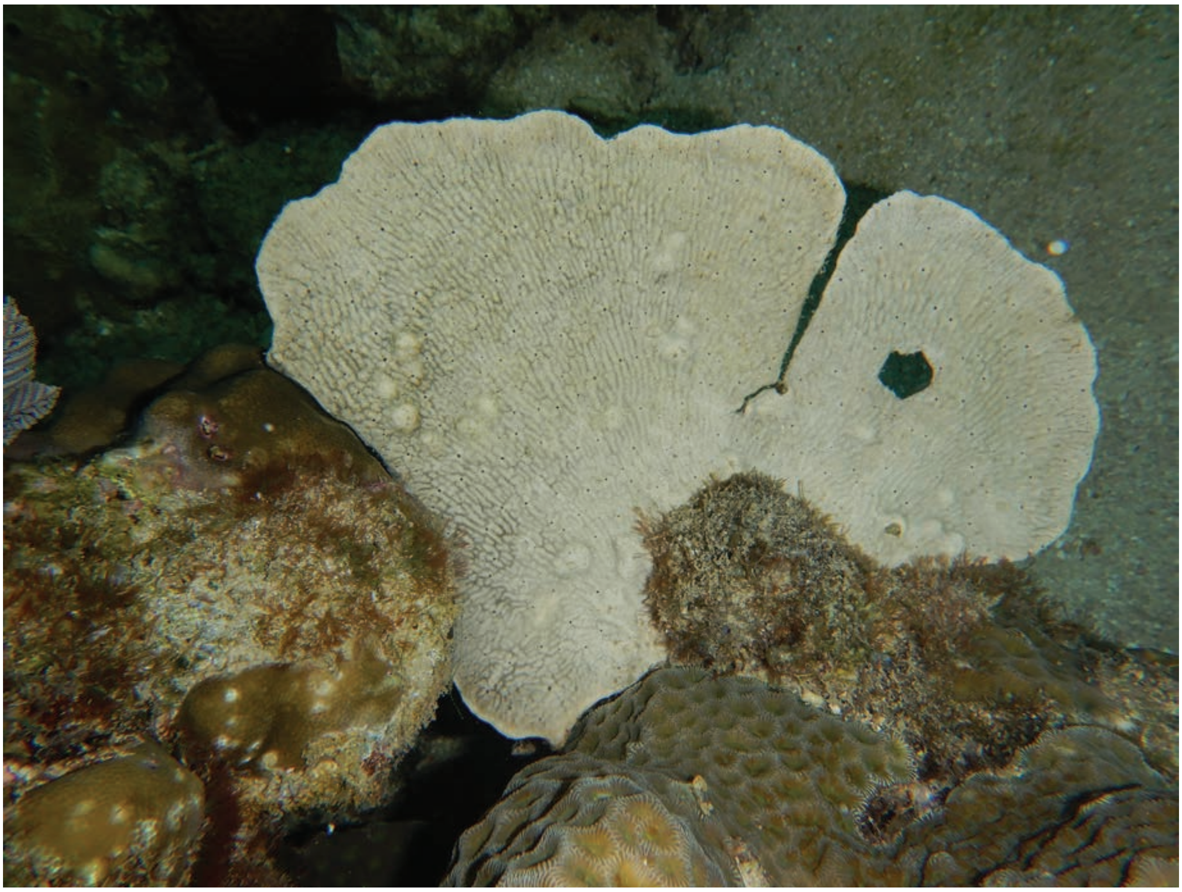


Figure 26. Habitus in situ of *Phyllospongia foliascens* (Pallas, 1766) at Samalona Island, the Spermonde Archipelago (photograph by SAP).

al. 1988; Abdul Wahab et al. 2021). *Phyllospongia foliascens* is a phototrophic species that mainly relies on symbiotic cyanobacteria for its nutrient cycle. This species is also able to endure high energy environments (Cleary et al. 2005).

Distribution and ecology. Numerous individuals were found during the survey. *Phyllospongia foliascens* is widely distributed and has a high density in the Spermonde Archipelago (de Voogd et al. 2006). Our specimen was found at south-west of Samalona Island, reef flat; Gusung Tallang, turbid reef. This species has been recorded from shallow waters of the Red Sea, Indian Ocean, Australia, and Fiji (Abdul Wahab et al. 2021).

Discussion

Twenty-seven species of marine sponges (Class Calcarea and Class Demospongiae) have been identified in the littoral area of the Spermonde Archipelago, Indonesia. The Order Haplosclerida, with nine species, dominates this type of habitat. According to the WPD checklist (de Voogd et al. 2024), some of the sponges found here, such as *Clathrina rodriguesensis*, *Amphimedon paraviridis*, *Niphates nitida*, and *Ircinia schulzei*, are newly recorded for Indonesia. Several others are new records for the Sulawesi Sea/Makassar Strait marine ecoregion, including *Janusya tubuloreticulosa*, *Leucaltis nodusgordii*, *Spirastrella* aff. *decumbens*, *Haliclona* (*Reniera*) *venusta*, *Haliclona* (*Soestella*) *elegantia*, *Lissodendoryx* (*Waldoschmittia*) *schmidti*, *Halichondria* (*Halichondria*) *cartilaginea*, and *Topsentia indica* (Suppl. material 2). Four species potentially new to science are also preliminarily described; further examination, including molecular analysis, is needed to accurately describe all the species.

In relation to extreme habitats, several species such as *Phyllospongia foliascens*, *Stylissa massa*, *Clathria* (*Thalysias*) *reinwardti*, and *Haliclona* (*Gellius*) *cymaeformis* are frequently found in this habitat (Suppl. material 3). For instance, the foliose sponge *Phyllospongia foliascens* as well as *Haliclona* (*Gellius*) *cymaeformis* were very abundant in the turbid reef near Makassar city, e.g., Kayangan Island, Gusung Tallang, and Samalona Island (SAP pers. obs. 2020). This habitat is unusual for phototropic species. Studies in other areas (i.e., north-west Java, the Great Barrier Reef) have shown that they are typically found in oligotrophic environments, characterized by low concentrations of organic nutrients (Wilkinson 1988; de Voogd and Cleary 2008). Conversely, several variables could be influencing the presence of these species in this unique environment. This could also be altered by algal symbionts that provide all the required carbon through photosynthesis, and the nitrogen from heterotrophic sources such as ultra-plankton (Davy et al. 2002; Pile et al. 2003).

Several species mentioned above, including *Paratetilla bacca*, *Spirastrella decumbens*, and *Petrosia* (*Petrosia*) *hoeksemai*, have demonstrated preferences for sedimented environments (Putchakarn 2011; Schönberg 2021). Although psammobiotic species typically exhibit an affinity for sedimented habitats (Schönberg 2016), sediment presence can exert negative pressures on sponge communities. Specifically, when subjected to elevated concentrations of suspended sediment, sponge taxa can exhibit diminished pumping activity and reduced feeding efficiency (Lohrer et al. 2006). Moreover, there may be alterations in their respiration rates (Pineda et al. 2017) and tissue abrasion (Nava and Carballo 2013). Such physiological stressors can culminate in partial mortality and compromised survival rates. A decline in sponge abundance, biomass, and species diversity has the potential to instigate cascading effects on broader marine ecosystems (Bell 2008).

Conclusions

In the littoral area, sponges predominantly colonize coral matrices and other hard substrates. Our recent investigation uncovers previously undocumented occurrences, including potentially new taxa, within the sponge community residing in the Sulawesi Sea/Makassar Strait marine ecoregion, particularly at the Spermonde Archipelago, SW Sulawesi. Noteworthy findings include the identification of 15 new records for the marine ecoregion, bringing the total to 143 species on the checklist, not including four potentially novel species. The sponge assemblage within this archipelago presents a rich and intricate biodiversity, underscoring an immediate imperative for comprehensive characterization. Rigorous examination coupled with molecular analysis of specimens is essential to ensure description of the entire species set.

Acknowledgements

This study formed part of the first author's (SAP) PhD research at Hasanuddin University. The authors would like to thank the Ministry of Education, Culture, Research, and Technology of Indonesia (KEMENDIKBUDRISTEK) for the PhD dissertation research funding (*Bantuan Penelitian Disertasi Doktor*) of the fiscal year 2022–2023 under decree 033/E5/PG.02.00/2022 (Nomor Surat: 0267/E5/AK.04/2022), awarded to RAR. We also thank 4D-REEF, www.4d-reef.eu (the European Union's Horizon 2020 research and innovation programme under the Marie Sklodowska-Curie grant agreement No. 813360) for making this collaboration possible. Additionally, we would like to thank the reviewers for their valuable suggestions and the subject editor for their assistance during the peer review process.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This work was supported by Kementerian Riset Teknologi Dan Pendidikan Tinggi Republik Indonesia.

Author contributions

Conceptualization: SAAP, JJ. Data curation: NJJV. Formal analysis: SAAP. Funding acquisition: RAR. Investigation: SAAP. Methodology: RAR. Resources: RAR. Supervision: JJ, RAR, NJJV. Validation: NJJV. Writing - original draft: SAAP. Writing - review and editing: RAR, NJJV, JJ.

Author ORCIDs

Singgih Afifa Putra https://orcid.org/0000-0003-1945-7513
Rohani Ambo-Rappe https://orcid.org/0000-0001-9276-7492

Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

References

Abdul Wahab MA, Wilson NG, Prada D, Gomez O, Fromont J (2021) Molecular and morphological assessment of tropical sponges in the subfamily Phyllospongiinae, with the descriptions of two new species. Zoological Journal of the Linnean Society 193(1): 319–335. https://doi.org/10.1093/zoolinnean/zlaa133

Alvarez B, Hooper JNA (2011) Taxonomic revision of the order Halichondrida (Porifera: Demospongiae) of northern Australia. Family Halichondriidae. Beagle 27: 55–84. https://doi.org/10.5962/p.287472

Alvarez B, de Voogd NJ, van Soest RWM (2016) Sponges of the family Axinellidae (Porifera: Demospongiae) in Indonesia. Zootaxa 4137(4): 451–477. https://doi.org/10.11646/zootaxa.4137.4.1

Azzini F, Calcinai B, Cerrano C, Bavestrello G, Pansini M (2007) Sponges of the marine karst lakes and of the coast of the islands of Ha Long Bay (North Vietnam). In: Custódio MR, Lôbo-Hajdu G, Hajdu E, Muricy G (Eds) Porifera Research: Biodiversity, Innovation and Sustainability. Museu Nacional (Brasil), Rio de Janeiro, 157–164. https://www.marinespecies.org/aphia.php?p=sourcedetails&id=283141 [accessed 15-10-2019]

Baer L (1906) Silicispongien von Sansibar, Kapstadt and Papeete. (Inaugural Dissertation: Berlin). Archiv für Naturgeschichte 72: 1–32 [pls I–V]. https://www.marinespecies.org/aphia.php?p=sourcedetails&id=7090 [accessed 22-05-2021]

Becking LE (2013) Revision of the genus *Placospongia* (Porifera, Demospongiae, Hadromerida, Placospongiidae) in the Indo-West Pacific. ZooKeys 298: 39–76. https://doi.org/10.3897/zookeys.298.1913

Becking LE, Lim SC (2009) A new *Suberites* (Demospongiae: Hadromerida: Suberitidae) from the tropical Indo-West Pacific. Zoölogische Mededeelingen 83: 853–862. Available from https://repository.naturalis.nl/pub/315882/

Bell JJ (2008) The functional roles of marine sponges. Estuarine, Coastal and Shelf Science 79(3): 341–353. https://doi.org/10.1016/j.ecss.2008.05.002

Bergquist PR (1965) The Sponges of Micronesia, Part I. The Palau Archipelago. Pacific Science XIX: 123–204. https://biostor.org/reference/234177

Bergquist PR, Ayling AM, Wilkinson CR (1988) Foliose Dictyoceratida of the Australian Great Barrier Reef. Marine Ecology 9(4): 291–319. https://doi.org/10.1111/j.1439-0485.1988.tb00209.x

Boury-Esnault N, Rützler K (1997) Thesaurus of sponge morphology. Smithsonian Contributions to Zoology 596(596): 1–55. https://doi.org/10.5479/si.00810282.596

Bowerbank JS (1875) Contributions to a General History of the Spongiadae. Part VII. Proceedings of the Zoological Society of London, 281–296. http://www.marinespecies.org/aphia.php?p=sourcedetails&id=7225

Burt JA, Camp EF, Enochs IC, Johansen JL, Morgan KM, Riegl B, Hoey AS (2020) Insights from extreme coral reefs in a changing world. Coral Reefs 39(3): 495–507. https://doi.org/10.1007/s00338-020-01966-y

Cairns SD (1999) Species richness of recent Scleractinia. Atoll Research Bulletin 459: 1–46. https://doi.org/10.5479/si.00775630.459.1

Calcinai B, Bavestrello G, Cerrano C (2005) Excavating sponge species from the Indo-Pacific Ocean. Zoological Studies 44: 5–18. https://zoolstud.sinica.edu.tw/Journals/44.1/5.html

Calcinai B, Azzini F, Bavestrello G, Cerrano C, Pansini M, Thung DC (2006) Boring sponges from Ha Long Bay, Tonkin Gulf, Vietnam. Zoological Studies (Taipei, Taiwan) 45: 201–212. https://zoolstud.sinica.edu.tw/Journals/45.2/201.html

Calcinai B, Bastari A, Bavestrello G, Bertolino M, Horcajadas SB, Pansini M, Makapedua DM, Cerrano C (2017) Demosponge diversity from North Sulawesi, with the description of six new species. ZooKeys 680: 105–150. https://doi.org/10.3897/zookeys.680.12135

Cárdenas P, Gamage J, Hettiarachchi CM, Gunasekera S (2022) Good practices in sponge natural product studies: Revising vouchers with isomalabaricane triterpenes. Marine Drugs 20(3): 190. https://doi.org/10.3390/md20030190

Cleary DFR, Becking LE, de Voogd NJ, Renema W, de Beer M, van Soest RWM, Hoeksema BW (2005) Variation in the diversity and composition of benthic taxa as a function of distance offshore, depth and exposure in the Spermonde Archipelago, Indonesia. Estuarine, Coastal and Shelf Science 65(3): 557–570. https://doi.org/10.1016/j.ecss.2005.06.025

Davy SK, Trautman DA, Borowitzka MA, Hinde R (2002) Ammonium excretion by a symbiotic sponge supplies the nitrogen requirements of its rhodophyte partner. The Journal of Experimental Biology 205(22): 3505–3511. https://doi.org/10.1242/jeb.205.22.3505

de C. Cook S, Bergquist PR (1999) New species of dictyoceratid sponges from New Zealand: Genus *Ircinia* (Porifera: Demospongiae: Dictyoceratida). New Zealand Journal of Marine and Freshwater Research 33: 545–563. https://doi.org/10.1080/00288330.1999.9516899

de Laubenfels MW (1954) The Sponges of the West-Central Pacific. Oregon State College, Oregon, 336 pp. https://doi.org/10.5962/bhl.title.6516 [accessed 10-09-2019]

de Voogd NJ (2004) *Callyspongia* (*Euplacella*) *biru* spec. nov. (Porifera: Demospongiae: Haplosclerida) from Indonesia. Zoölogische Mededeelingen 78: 477–483. https://repository.naturalis.nl/pub/214454

de Voogd NJ (2005) Indonesian Sponges: Biodiversity and Mariculture Potential. University of Amsterdam. https://hdl.handle.net/11245/1.237560 [accessed 24-09-2019]

de Voogd NJ, Cleary DFR (2008) An analysis of sponge diversity and distribution at three taxonomic levels in the Thousand Islands/Jakarta Bay reef complex, West-Java, Indonesia. Marine Ecology 29(2): 205–215. https://doi.org/10.1111/j.1439-0485.2008.00238.x

de Voogd NJ, van Soest RWM (2002) Indonesian sponges of the genus *Petrosia* Vosmaer (Demospongiae: Haplosclerida). Zoologische Mededelingen (Leiden) 76: 193–209. https://hdl.handle.net/11245/1.197534 [accessed 13-10-2019]

de Voogd NJ, van Soest RWM, Hoeksema BW (1999) Cross shelf distribution patterns of reef sponges of SW Sulawesi. Memoirs of the Queensland Museum 44: 147–154. https://hdl.handle.net/11245/1.158343

de Voogd NJ, Cleary D, Hoeksema B, Noor A, van Soest RWM (2006) Sponge beta diversity in the Spermonde Archipelago, SW Sulawesi, Indonesia. Marine Ecology Progress Series 309: 131–142. https://doi.org/10.3354/meps309131

de Voogd NJ, Alvarez B, Boury-Esnault N, Cárdenas P, Díaz M-C, Dohrmann M, Downey R, Goodwin C, Hajdu E, Hooper JNA, Kelly M, Klautau M, Lim SC, Manconi R, Morrow

C, Pinheiro U, Pisera AB, Ríos P, Rützler K, Schönberg C, Turner T, Vacelet J, van Soest RWM, Xavier J (2024) World Porifera Database. https://doi.org/10.14284/359 [accessed 02-05-2024]

de Weerdt WH (2000) A monograph of the shallow-water Chalinidae (Porifera, Haplosclerida) of the Caribbean. Beaufortia 50: 1–67. http://www.repository.naturalis.nl/record/505081

de Weerdt WH, van Soest RWM (2001) *Haliclona* (*Halichoclona*) *vanderlandi* spec. nov. (Porifera: Demospongiae: Haplosclerida) from Indonesia. Zoölogische Verhandelingen 334: 189–194. https://hdl.handle.net/11245/1.182998

Dendy A (1905) Report on the sponges collected by Professor Herdman at Ceylon in 1902. In: Herdman WA (Ed.) Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar. 3 (Supplement 18). Royal Society, London, 57–246 [pls I–XVI]. https://www.marinespecies.org/aphia.php?p=sourcedetails&id=7402 [accessed 18-09-2020]

Erpenbeck D, Hooper JNA, Bonnard I, Sutcliffe P, Chandra M, Perio P, Wolff C, Banaigs B, Wörheide G, Debitus C, Petek S (2012) Evolution, radiation and chemotaxonomy of *Lamellodysidea*, a demosponge genus with anti-plasmodial metabolites. Marine Biology 159(5): 1119–1127. https://doi.org/10.1007/s00227-012-1891-z

Erpenbeck D, Aryasari R, Benning S, Debitus C, Kaltenbacher E, Al-Aidaroos AM, Schupp P, Hall K, Hooper JNA, Voigt O, de Voogd NJ, Wörheide G (2017) Diversity of two widespread Indo-Pacific demosponge species revisited. Marine Biodiversity 47(4): 1035–1043. https://doi.org/10.1007/s12526-017-0783-3

Fromont J (1993) Descriptions of species of the Haplosclerida (Porifera: Demospongiae) occurring in tropical waters of the Great Barrier Reef. The Beagle, Records of the Northern Territory Museum of Arts and Sciences 10: 7–40. https://doi.org/10.5962/p.271278 [accessed 22-04-2021]

Fromont J, Sampey A (2014) Kimberley marine biota. Historical data: Sponges (Porifera). Records of the Western Australian Museum 84: 69–100. https://doi.org/10.18195/issn.0313-122x.84.2014.069-100

Fromont J, Richards ZT, Wilson NG (2019) First Report of the Coral-Killing Sponge *Terpios hoshinota* Rützler and Muzik, 1993 in Western Australia: A New Threat to Kimberley Coral Reefs? Diversity 11(10): 184. https://doi.org/10.3390/d11100184

George AM, van Soest RWM, Sluka RD, Lazarus Z (2020) A checklist of marine sponges (Porifera) of peninsula India. Zootaxa 4885(2): 277–300. https://doi.org/10.11646/zootaxa.4885.2.10

Hentschel E (1912) Kiesel- und Hornschwämme der Aru- und Kei-Inseln. Abhandlungen herausgegeben von der Senckenbergischen naturforschenden Gesellschaft 34: 293–448 [pls 13–21]. http://www.marinespecies.org/porifera/porifera.php?p=sourcedetails&id=7613 [accessed 07-01-2020]

Hofman CC, van Soest RWM (1995) *Lissodendoryx* species of the Indo-Malayan Archipelago (Demospongiae: Poecilosclerida). Beaufortia 45: 77–103. https://repository.naturalis.nl/pub/505066

Hooper JNA (1996) Revision of Microcionidae (Porifera: Poecilosclerida: Demospongiae), with Description of Australian Species. Memoirs of the Queensland Museum 40: 1–626. https://biostor.org/reference/105277

Hooper JNA (2003) 'Sponguide'. Guide To Sponge Collection and Identification. South Brisbane. https://www.researchgate.net/publication/242495363_Sponguide_Guide_to_Sponge_Collection_and_Identification [accessed 10-09-2019]

Hooper JNA (2008) Sponges. In: Hutchings P, Kingsford MJ, Hoegh-Guldberg IO (Eds) The Great Barrier Reef Biology, Environment and Management. CSIRO Publishing, Melbourne, 170–186. https://ebooks.publish.csiro.au/content/great-barrier-reef-9781486308200 [accessed 19-06-2024]

Hooper JNA, van Soest RWM [Eds] (2002) Systema Porifera. A Guide to the Classification of Sponges. Vol. 1–2. Springer US, Boston, MA, 1708 pp. https://doi.org/10.1007/978-1-4615-0747-5

Hopley D (2011) Encyclopedia of Modern Coral Reefs. Encyclopedia of Earth Sciences Series Encyclopedia of Modern Coral Reefs. Hopley D (Ed.) Springer Netherlands, Dordrecht, 405–449 pp. https://doi.org/10.1007/978-90-481-2639-2

Huang YM, de Voogd NJ, Cleary DFR, Li TH, Mok HK, Ueng JP (2016) Biodiversity pattern of subtidal sponges (Porifera: Demospongiae) in the Penghu Archipelago (Pescadores), Taiwan. Journal of the Marine Biological Association of the United Kingdom 96(2): 417–427. https://doi.org/10.1017/S002531541500017X

Immanuel T, Krishnan P, Raghunathan C (2015) An Updated Report on the Diversity of Marine Sponges of the Andaman and Nicobar Islands. In: Marine Faunal Diversity in India. Elsevier, 3–13. https://doi.org/10.1016/B978-0-12-801948-1.00001-X

Kench PS, Mann T (2017) Reef Island evolution and dynamics: Insights from the Indian and Pacific Oceans and Perspectives for the Spermonde Archipelago. Frontiers in Marine Science 4: 145. https://doi.org/10.3389/fmars.2017.00145

Kieschnick O (1896) Silicispongiae von Ternate nach den Sammlungen von Herrn Prof. Dr. W. Kükenthal. Zoologischer Anzeiger 19: 526–534. https://www.marinespecies.org/aphia.php?p=sourcedetails&id=7713

Kusumoto B, Costello MJ, Kubota Y, Shiono T, Wei CL, Yasuhara M, Chao A (2020) Global distribution of coral diversity: Biodiversity knowledge gradients related to spatial resolution. Ecological Research 35(2): 315–326. https://doi.org/10.1111/1440-1703.12096

Li T-H (2013) Preliminary survey on the biodiversity of marine sponges (Porifera: Demospongiae) in the Southern Water off Penghu Archipelago. National Sun Yat-sen University. https://hdl.handle.net/11296/2sn4n6 [accessed 28-02-2022]

Lim SC, de Voogd NJ, Tan KS (2012) Biodiversity of shallow-water sponges (Porifera) in Singapore and description of a new species of *Forcepia* (Poecilosclerida: Coelosphaeridae). Contributions to Zoology 81(1): 55–71. https://doi.org/10.1163/18759866-08101004

Lim SC, Putchakarn S, Thai MQ, Wang D, Huang YM (2016) Inventory of sponge fauna from the Singapore Strait to Taiwan Strait along the western coastline of the South China Sea. The Raffles Bulletin of Zoology Supplement No. 34, 104–129. https://lkcnhm.nus.edu.sg/publications/raffles-bulletin-of-zoology/supplements/supplement-no-34/

Lindgren NG (1898) Beitrag zur Kenntniss der Spongienfauna des Malayischen Archipels und der chinesischen Meere. Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Thiere 11: 283–378 [pls 17–20]. https://www.marinespecies.org/aphia.php?p=sourcedetails&id=7886 [accessed 13-09-2021]

Lohrer A, Hewitt J, Thrush S (2006) Assessing far-field effects of terrigenous sediment loading in the coastal marine environment. Marine Ecology Progress Series 315: 13–18. https://doi.org/10.3354/meps315013

Longakit MBA, Sotto FB, Kelly M (2005) The shallow water marine sponges (Porifera) of Cebu, Philippines. Science Diliman 17: 52–74. https://journals.upd.edu.ph/index.php/sciencediliman/article/view/59

Łukowiak M, van Soest RWM, Klautau M, Pérez T, Pisera A, Tabachnick K (2022) The terminology of sponge spicules. Journal of Morphology 283(12): 1517–1545. https://doi.org/10.1002/jmor.21520

Montano S, Reimer JD, Ivanenko VN, García-Hernández JE, van Moorsel GWNM, Galli P, Hoeksema BW (2020) Widespread Occurrence of a Rarely Known Association between the Hydrocorals *Stylaster roseus* and *Millepora alcicornis* at Bonaire, Southern Caribbean. Diversity 12(6): 218. https://doi.org/10.3390/d12060218

Nava H, Carballo JL (2013) Environmental factors shaping boring sponge assemblages at Mexican Pacific coral reefs. Marine Ecology 34(3): 269–279. https://doi.org/10.1111/maec.12012

Núñez Pons L, Calcinai B, Gates RD (2017) Who's there? – First morphological and DNA barcoding catalogue of the shallow Hawai'ian sponge fauna. PLoS ONE 12(12): e0189357. https://doi.org/10.1371/journal.pone.0189357

Parenden D, Jompa J, Rani C (2021) Condition of hard corals and quality of the turbid waters in Spermonde Islands (Case studies in Kayangan Island, Samalona Island and Kodingareng Keke Island). IOP Conference Series. Earth and Environmental Science 921(1): 012060. https://doi.org/10.1088/1755-1315/921/1/012060

Pattengill-Semmens C (2001) Learning to see underwater. Underwater Naturalist 25: 37–40. https://www.reef.org/news/publications/learning-see-underwater

Pile AJ, Grant A, Hinde R, Borowitzka MA (2003) Heterotrophy on ultraplankton communities is an important source of nitrogen for a sponge-rhodophyte symbiosis. The Journal of Experimental Biology 206(24): 4533–4538. https://doi.org/10.1242/jeb.00698

Pineda M-C, Strehlow B, Sternel M, Duckworth A, Jones R, Webster NS (2017) Effects of suspended sediments on the sponge holobiont with implications for dredging management. Scientific Reports 7(1): 4925. https://doi.org/10.1038/s41598-017-05241-z

Polónia ARM, Cleary DFR, de Voogd NJ, Renema W, Hoeksema BW, Martins A, Gomes NCM (2015) Habitat and water quality variables as predictors of community composition in an Indonesian coral reef: A multi-taxon study in the Spermonde Archipelago. The Science of the Total Environment 537: 139–151. https://doi.org/10.1016/j.scitotenv.2015.07.102

Pulitzer-Finali G (1993) A collection of marine sponges from East Africa. Annali del Museo Civico di Storia Naturale "Giacomo Doria" 89: 247–350. https://www.marinespecies.org/aphia.php?p=sourcedetails&id=6217 [accessed 25-05-2021]

Pulitzer-Finali G, Pronzato R (1999) Horny sponges from the north-eastern coast of Papua New Guinea, Bismark Sea. Journal of the Marine Biological Association of the United Kingdom 79(4): 593–607. https://doi.org/10.1017/S0025315498000769

Putchakarn S (2007) Species diversity of marine sponges dwelling in coral reefs in Had Khanom—Mo Ko Thale Tai National Park, Nakhon Si Thammarat Province, Thailand. Journal of the Marine Biological Association of the United Kingdom 87(6): 1635–1642. https://doi.org/10.1017/S002531540705833X

Putchakarn S (2011) Species diversity of marine sponges along Chanthaburi and Trat Provinces, the Eastern Coast of the Gulf of Thailand. Publications of the Seto Marine Biological Laboratory 41: 17–23. https://doi.org/10.5134/159486

Putra SA, Ambo-Rappe R, Jompa J, de Voogd NJ (2023) Two centuries of sponges (phylum Porifera) taxonomic studies in Indonesia (1820–2021): Checklist and bibliography. Zootaxa 5298(1): 1–74. https://doi.org/10.11646/zootaxa.5298.1.1

Reimer JD, Wee HB, García-Hernández JE, Hoeksema BW (2018) Zoantharia (Anthozoa: Hexacorallia) abundance and associations with Porifera and Hydrozoa across a depth gradient on the west coast of Curaçao. Systematics and Biodiversity 16(8): 820–830. https://doi.org/10.1080/14772000.2018.1518936

Ridley SO (1884) Spongiida. Report on the Zoological Collections made in the Indo-Pacific Ocean during the Voyage of H.M.S. 'Alert', 1881–2. (British Museum (Natural History): London)., 366–482 [pls 39–43; 582–630, 53–54]. http://www.marinespecies.org/aphia.php?p=sourcedetails&id=8099 [accessed 14-07-2021]

Row RWH (1911) Reports on the Marine Biology of the Sudanese Red Sea, from Collections made by Cyril Crossland, M.A., B.Sc., F.Z.S. XIX. Report on the Sponges collected by Mr. Cyril Crossland in 1904–5. Part II. Non-Calcarea. Journal of the Linnean Society. Zoology. 31: 287–400 [pls 35–41]. https://doi.org/10.1111/j.1096-3642.1911.tb00461.x [accessed 19-04-2022]

Rützler K (1974) The burrowing sponges of Bermuda. Smithsonian Contributions to Zoology 165(165): 1–32. https://doi.org/10.5479/si.00810282.165

Rützler K (2004) Sponges on coral reefs: a community shaped by competitive cooperation. Bolletino di Museo e Istituto di Biologia dell'Universita di Genova 68: 85–148. http://si-pddr.si.edu/jspui/handle/10088/163 [accessed 10-09-2019]

Rützler K, Muzik K (1993) *Terpios hoshinota*, a new cyanobacteriosponge threatening Pacific reefs. Scientia Marina 57: 395–403. https://repository.si.edu/handle/10088/7882

Samaai T, Pillay R, Janson L (2019) Shallow-water Demospongiae (Porifera) from Sodwana Bay, iSimangaliso Wetland Park, South Africa. Zootaxa 4587(1): 1–85. https://doi.org/10.11646/zootaxa.4587.1.1

Santodomingo N, Becking LE (2018) Unravelling the moons: Review of the genera *Paratetilla* and *Cinachyrella* in the Indo-Pacific (Demospongiae, Tetractinellida, Tetillidae). ZooKeys 791: 1–46. https://doi.org/10.3897/zookeys.791.27546

Sari NWP, Siringoringo RM, Abrar M, Putra RD, Sutiadi R, Yusuf S (2021) Status of coral reefs in the water of Spermonde, Makassar, South Sulawesi. [Jameson G, Gibson I, Feng LW, Yamamoto T, Pardi H (Eds)]. E3S Web of Conferences 324: 03007. https://doi.org/10.1051/e3sconf/202132403007

Schönberg CHL (2016) Happy relationships between marine sponges and sediments – a review and some observations from Australia. Journal of the Marine Biological Association of the United Kingdom 96(2): 493–514. https://doi.org/10.1017/S0025315415001411

Schönberg CHL (2021) No taxonomy needed: Sponge functional morphologies inform about environmental conditions. Ecological Indicators 129: 107806. https://doi.org/10.1016/j.ecolind.2021.107806

Sollas WJ (1888) Report on the Tetractinellida collected by H.M.S. Challenger, during the years 1873–1876. Report on the Scientific Results of the Voyage of H.M.S. Challenger During the Years 1873–76 25: 284–346. http://www.19thcenturyscience.org/HMSC/HMSC-Reports/Zool-63/htm/doc.html [accessed 28-01-2021]

Spalding MD, Fox HE, Allen GR, Davidson N, Ferdaña ZA, Finlayson M, Halpern BS, Jorge MA, Lombana A, Lourie SA, Martin KD, McManus E, Molnar J, Recchia CA, Robertson J (2007) Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas. Bioscience 57(7): 573–583. https://doi.org/10.1641/B570707

Syue S-T, Hsu C-H, Soong K (2021) Testing of how and why the *Terpios hoshinota* sponge kills stony corals. Scientific Reports 11(1): 7661. https://doi.org/10.1038/s41598-021-87350-4

Thiele J (1899) Studien über pazifische Spongien. II. Ueber einige Spongien von Celebes. Original-Abhandlungen aus dem Gesamtgebiete der Zoologie. Stuttgart 24: 1–33. http://www.marinespecies.org/porifera/porifera.php?p=sourcedetails&id=8296 [accessed 25-12-2019]

Thiele J (1900) Kieselschwämme von Ternate. I. Abhandlungen herausgegeben von der Senckenbergischen naturforschenden Gesellschaft. Frankfurt 25: 19–80. http://www.marinespecies.org/porifera/porifera.php?p=sourcedetails&id=8297 [accessed 06-12-2019]

Thomas PA (1973) Marine Demospongiae of Mahe Island in the Seychelles Bank (Indian Ocean). Zoologische Wetenschappen 203: 1–96. http://eprints.cmfri.org.in/7923/ [accessed 15-10-2019]

Thomas PA (1986) Demospongiae of Minicoy Island (Indian Ocean) - Part 2. Order Poecilosclerida. Journal of the Marine Biological Association of India 12: 1–7. https://www.marinespecies.org/aphia.php?p=sourcedetails&id=133506

Thomas PA (1991) Sponges of Papua and New Guinea - Part Order Haplosclerida Topsent. Journal of the Marine Biological Association of India 33: 308–316. https://www.marinespecies.org/aphia.php?p=sourcedetails&id=148309

Topsent E (1897) Spongiaires de la Baie d'Amboine. (Voyage de MM. M. Bedot et C. Pictet dans l'archipel Malais). Revue Suisse de Zoologie 4(3): 421–487. https://doi.org/10.5962/bhl.part.35507

Umbgrove JHF (1928) De koraalriffen van den Spermonde- Archipel (Zuid-Celebes). Leidse Geologische Mededelingen 3: 228–247. https://www.repository.naturalis.nl/record/505609 [accessed 12-04-2020]

Uriz MJ (2002) Family Ancorinidae Schmidt, 1870. In: Hooper JNA, van Soest RWM (Eds) Systema Porifera: A Guide to the Classification of Sponges. Kluwer Academic/Plenum Publisher, New York, 108–126. https://doi.org/10.1007/978-1-4615-0747-5_12

Vacelet J, Vasseur P, Levi C (1976) Spongiaires de la pente externe des récifs coralliens de Tulear (sud-ouest de Madagascar). Mémoires du Muséum National d'histoire Naturelle (A. Zoologie) 49: 1–116. https://www.biodiversitylibrary.org/part/282220 [accessed 19-04-2022]

van Soest RWM (1990) Shallow water reef sponges of Eastern Indonesia. In: Rützler K (Ed.) New Perspectives in Sponge Biology. Smithsonian Institution Press, Washington, D.C., 302–308. https://hdl.handle.net/11245/1.424105 [accessed 18-06-2024]

van Soest RWM, de Voogd NJ (2015) Calcareous sponges of Indonesia. Zootaxa 3951(1): 1–105. https://doi.org/10.11646/zootaxa.3951.1.1

van Soest RWM, de Voogd NJ (2018) Calcareous sponges of the Western Indian Ocean and Red Sea. Zootaxa 4426(1): 160. https://doi.org/10.11646/zootaxa.4426.1.1

van Soest RWM, Hooper JNA, Butler PJ (2020) Every sponge its own name: Removing Porifera homonyms. Zootaxa 4745(1): 1–93. https://doi.org/10.11646/zootaxa.4745.1.1

van Soest RWM, Aryasari R, de Voogd NJ (2021) *Mycale* species of the tropical Indo-West Pacific (Porifera, Demospongiae, Poecilosclerida). Zootaxa 4912(1): 1–212. https://doi.org/10.11646/zootaxa.4912.1.1

von Lendenfeld R (1903) Porifera. Tetraxonia. In: Schulze FE (Ed.) Das Tierreich 19. Friedländer, Berlin, 168 pp. http://www.marinespecies.org/porifera/porifera.php?p=sourcedetails&id=7831 [accessed 15-09-2021]

Wilkinson CR (1988) Foliose Dictyoceratida of the Australian Great Barrier Reef: II. Ecology and Distribution of these Prevalent Sponges. Marine Ecology 9(4): 321–327. https://doi.org/10.1111/j.1439-0485.1988.tb00210.x

Williams GJ, Graham NAJ, Jouffray JB, Norström AV, Nyström M, Gove JM, Heenan A, Wedding LM (2019) Coral reef ecology in the Anthropocene. Functional Ecology 33(6): 1014–1022. https://doi.org/10.1111/1365-2435.13290

Wilson HV (1925) Silicious and horny sponges collected by the U.S. Fisheries Steamer "Albatross" during the Philippine Expedition, 1907–1910. Bulletin of the United States National Museum. Contributions to the biology of the Philippine Archipelago and adjacent regions 100: 273–532. https://repository.si.edu/handle/10088/21261 [accessed 12-04-2020]

Supplementary material 1

Sampling sites of sponge (Porifera) collections from shallow-subtidal habitat of the Spermonde Archipelago, Indonesia

Authors: Singgih Afifa Putra, Rohani Ambo-Rappe, Jamaluddin Jompa, Nicole J. de Voogd
Data type: docx

Link: https://doi.org/10.3897/zookeys.1208.113603.suppl1

Supplementary material 2

checklist of Porifera from Sulawesi Sea/Makassar Strait marine ecoregion with updates based on the current study

Authors: Singgih Afifa Putra, Rohani Ambo-Rappe, Jamaluddin Jompa, Nicole J. de Voogd
Data type: docx

Link: https://doi.org/10.3897/zookeys.1208.113603.suppl2

Supplementary material 3

List of sponge (Porifera) species examined in this study with locations and environmental condition in the Spermonde Archipelago, Indonesia

Authors: Singgih Afifa Putra, Rohani Ambo-Rappe, Jamaluddin Jompa, Nicole J. de Voogd
Data type: docx

Link: https://doi.org/10.3897/zookeys.1208.113603.suppl3

ZooKeys 1208: 315–330 (2024)
DOI: 10.3897/zookeys.1208.125938

Research Article

Five new species of the *Macrolycus ligulatus* species-group from China (Coleoptera, Lycidae)

Ruolan Du[1], Yuxia Yang[1,2], Xingke Yang[3], Haoyu Liu[1]

1 *Key Laboratory of Zoological Systematics and Application, School of Life Sciences, Hebei University, Baoding 071002, China*
2 *Hebei Basic Science Center for Biotic Interaction, Hebei University, Baoding 071002, China*
3 *Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China*
Corresponding authors: Yuxia Yang (yxyang@hbu.edu.cn); Haoyu Liu (liuhy@hbu.edu.cn)

Abstract

Five new species of the *Macrolycus ligulatus* species-group, *M. expansus* **sp. nov.**, *M. quartus* **sp. nov.**, *M. costus* **sp. nov.**, *M. opacipennis* **sp. nov.** and *M. curtus* **sp. nov.**, are reported from China and described with macrophotographs of the habitus of both sexes and aedeagi. *Macrolycus guangxiensis* Li, Bocak & Pang, 2015 is illustrated showing the female habitus and genitalia for the first time. In addition, a distribution map and a key to all species of the *M. ligulatus* species-group are provided.

Key words: Alpha taxonomy, China, Macrolycus, Net-winged beetles, new species

Academic editor: Vinicius S. Ferreira
Received: 22 April 2024
Accepted: 10 July 2024
Published: 1 August 2024

ZooBank: https://zoobank.org/48F428DA-4F53-4B37-AA3A-608A19B5F7D4

Citation: Du R, Yang Y, Yang X, Liu H (2024) Five new species of the *Macrolycus ligulatus* species-group from China (Coleoptera, Lycidae). ZooKeys 1208: 315–330. https://doi.org/10.3897/zookeys.1208.125938

Introduction

Net-winged beetles of the genus *Macrolycus* Waterhouse, 1878 sensu lato are widely distributed in the Oriental and eastern Palaearctic regions (Nakane 1969, 1994; Kazantsev 1993, 2001, 2002, 2013; Li et al. 2012, 2015; Liu et al. 2023; Du et al. 2024). It is the sole member of the tribe Macrolycini, currently placed in the subfamily Ateliinae Kleine, 1928 of Lycidae (Kusy et al. 2019). A total of 73 *Macrolycus* species have been recorded until now (Liu et al. 2023; Du et al. 2024), divided into nine species-groups based on molecular phylogeny (Li et al. 2015). Among them, the *M. ligulatus* species-group can be distinguished from others by the phallus usually expanded ventrodistally, and present with a U- or V-shaped notch and a tongue-like lamella at the apex (Li et al. 2015).

Eight species are currently included in the *M. ligulatus* species-group (Li et al. 2015). Recently, we assembled a large series of *Macrolycus* material from China and discovered dozens of new species that are currently being described or will be described based on their respective groups (Li et al. 2015). In this study, our focus lies on the *M. ligulatus* species-group, and we present five new species below.

Material and methods

The studied material is preserved in the Institute of Zoology, Chinese Academy of Sciences, Beijing, China (**IZAS**) and the Museum of Hebei University, Baoding, China (**MHBU**). We identified the species based on the works of Kazantsev (1993, 2001, 2002, 2013), Li et al. (2012, 2015) and Li (2015). The description format follows Li et al. (2012, 2015), and the terminology of female genitalia follows Kazantsev (2005).

The specimens were first softened in water, and then the genitalia of both sexes were dissected. After dissection, the male genitalia was cleared in 10% NaOH solution, examined and photographed in glycerol, and finally glued on a paper card for permanent preservation. The female genitalia was dyed with hematoxylin, examined in 75% alcohol and preserved in glycerol. Images of the adults were taken with a Canon EOS 80D digital camera and those of the genitalia by a Leica M205A stereomicroscope, which were stacked in Helicon Focus ver. 7. The final plates were edited in Adobe Photoshop CS3.10.0.1.

The measurements were taken with Image J ver. 1.50i (NIH, Bethesda, MD, USA). Body length was measured from the anterior margin of the head to the elytral apex, and the width across the elytral humeri. Pronotal length was measured from the middle of the anterior margin to the middle of the posterior margin of the pronotum, and the width across its widest part. Eye diameter was measured at the maximal width and the interocular distance at the minimal point. The length of the lamella of the antennae was measured from the apex to the middle of the joint itself. The aedeagus was measured and compared at the maximal width of the basal part, subapical part and apex in ventral views, respectively.

The distribution information was collected from the literature (Kazantsev 1993, 2001, 2013; Li et al. 2012, 2015; Li 2015) and the present studied material. The distribution map was prepared using ArcMap ver. 10.8 and edited in Photoshop CS3.10.0.1.

Results

Class Insecta Linnaeus, 1758
Order Coleoptera Linnaeus, 1758
Family Lycidae Laporte, 1836
Tribe Macrolycini Kleine, 1933
Genus *Macrolycus* Waterhouse, 1878

Macrolycus ligulatus species-group

Updated diagnosis. Female external genitalia (Fig. 1): valvifers free, styli slender and cylindrical, coxites elongate. Internal organ of female reproductive system (Fig. 1): vagina elongate and globular at apex, present with a pair of large vaginal pouches on both sides of the basal part and a pair of accessory glands, which are greatly expanded distad and separated on both sides of the apical part; seminal duct spiral tube-shaped; spermatheca rugby-shaped, present with a thin and bifurcate accessory gland arising from middle part. Male genitalia with phallus usually with a U- or V-shaped notch and a ventrally inclined and tapered or square lamella at apex (e.g., Figs 4, 6).

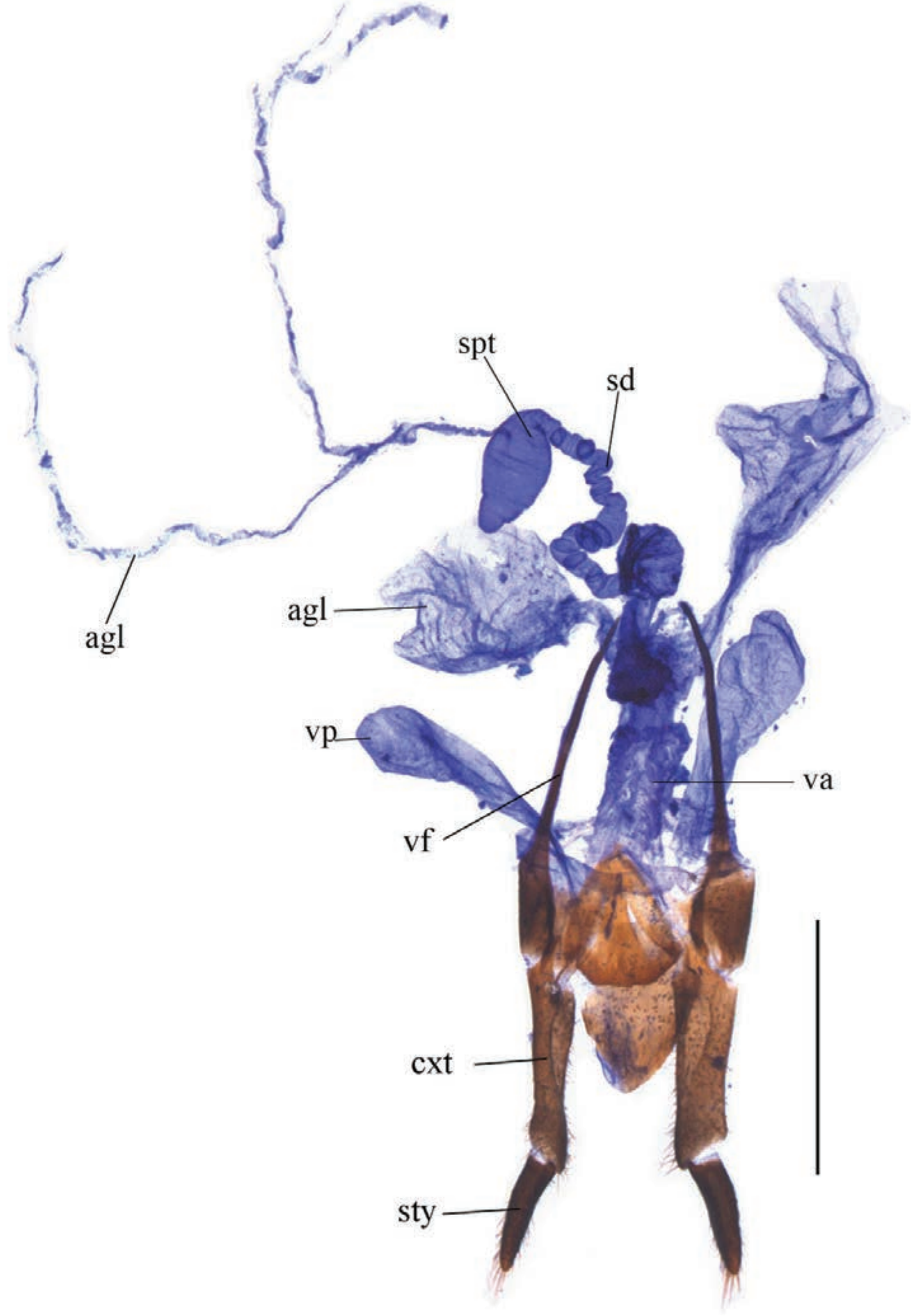


Figure 1. Internal organ of female reproductive system (ventral view) of *Macrolycus guangxiensis* Li, Bocak & Pang, 2015. Scale bars: 1.0 mm. Abbreviations: agl–accessory gland; va–vagina; vp–vaginal pouch; spt–spermatheca; sd–seminal duct; vf–valvifer; cxt– coxite; sty–stylus.

Included species. *Macrolycus notaticollis* Pic, 1935, *M. praecellens* Kazantsev, 1993, *M. bocakorum* Kazantsev, 2001, *M. extrusus* Li, Bocak & Pang, 2012, *M. ligulatus* Li, Bocak & Pang, 2012, *M. chapaensis* Kazantsev, 2013, *M. guangxiensis* Li, Bocak & Pang, 2015, *M. parvus* Li, Bocak & Pang, 2015, *M. expansus* sp. nov., *M. quartus* sp. nov., *M. costus* sp. nov., *M. opacipennis* sp. nov. and *M. curtus* sp. nov.

Distribution (Fig. 2). China (Ningxia, Gansu, Shaanxi, Sichuan, Guizhou, Zhejiang, Guangxi, Guangdong), Laos, Vietnam.

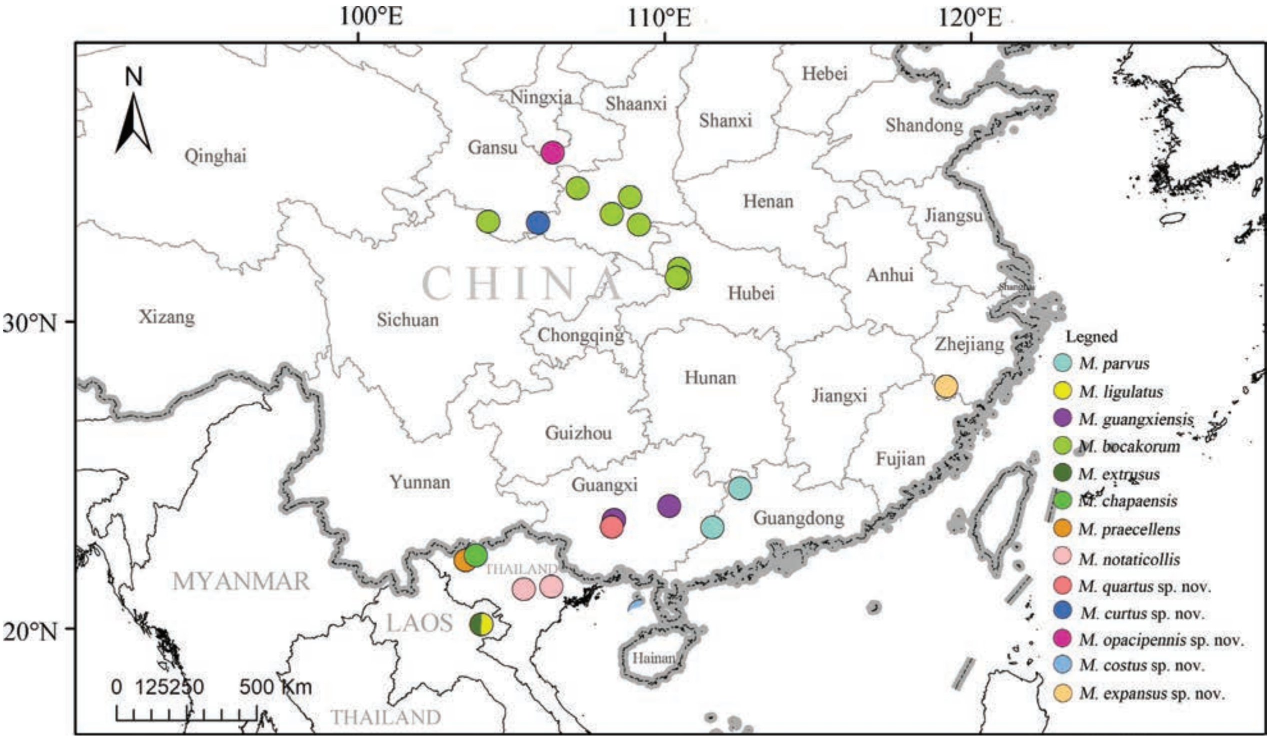


Figure 2. Distribution map of the *Macrolycus ligulatus* species-group in the world.

Remarks. The female reproductive system of *Macrolycus*, encompassing external genitalia and internal organs, with *M. guangxiensis* as the representative species, is presented here for the first time.

Macrolycus guangxiensis Li, Bocak & Pang, 2015

Figs 3A, 4A–C

Macrolycus guangxiensis Li, Bocak & Pang, 2015: 326, figs 9, 28, 29, 45, 55.

Material examined. China: 5♂8♀ (MHBU), Guangxi, Wuming, Damingshan, 1230– 1423 m, 20.v.2011, leg. H. Y. Liu.

Descriptive notes. Male. Phallus (Fig. 4A–C) slender, nearly parallel-sided at basal part in dorsal and ventral views (Fig. 4A, B), subapical part moderately and asymmetrically inflated laterally, about 1.45 times as wide as basal part, with an oval ventral-cavity, apical part progressively constricted distad, apex with a deep V-shaped notch, about 0.19 times as wide as subapical part; basal 1/3 part curved ventrally in lateral view (Fig. 4C), subapical part feebly inflated ventrally, apical part moderately expanded ventrally, and apex with a tapered lamella.

Female (Fig. 3A). Similar to males, but larger in body size. Length 11.8–13.2 mm, width at humeri 2.5–2.8 mm. Antennae serrate and antennomeres III–X long- or wide-triangular. Pronotum 1.2 times wider than long, anterior angles obtuse-angled. Elytra 3.6 times longer than humeral width.

Distribution (Fig. 2). China (Guangxi).

Remarks. We provide an illustration of the female habitus and a comparison with the males of this species for the first time.

Figure 3. Habitus, dorsal views of *Macrolycus guangxiensis* Li, Bocak & Pang, 2015 (**A**) and *M. expansus* sp. nov (**B**). **A** female **B** male. Scale bars: 1.0 mm.

Macrolycus expansus **Y. Yang, Liu & X. Yang, sp. nov.**

https://zoobank.org/9C3D89C2-894A-4C16-BAF9-831BD49827FD
Figs 3B, 4D–F

Diagnosis. The species resembles *M. guangxiensis* Li, Bocak & Pang, 2015 in the general shape of the phallus, but differs in the longer lamella of male antennomere III, 0.9 times as long as the joint itself (Fig. 3B); phallus with subapical part strongly inflated laterally in ventral view (Fig. 4E), apical part strongly expanded ventrally in lateral view (Fig. 4F). In comparison, in *M. guangxiensis* the lamella of male antennomere III is shorter and 0.7 times as long as the joint itself (Li et al. 2015: fig. 45), the subapical part of phallus is moderately inflated laterally in ventral view (Fig. 4B), and the apical part is moderately expanded ventrally in lateral view (Fig. 4C).

Etymology. The specific name is derived from the Latin *expansus* (to expand), referring to its strongly expanded subapical part of the phallus.

Type material. ***Holotype***. China: ♂ (IZAS), Zhejiang, Longquan, Fengyangshan, 29.vii.2007, leg. L. K Tan.

Description. Male (Fig. 3B). Length 9.3 mm, width at humeri 1.9 mm.

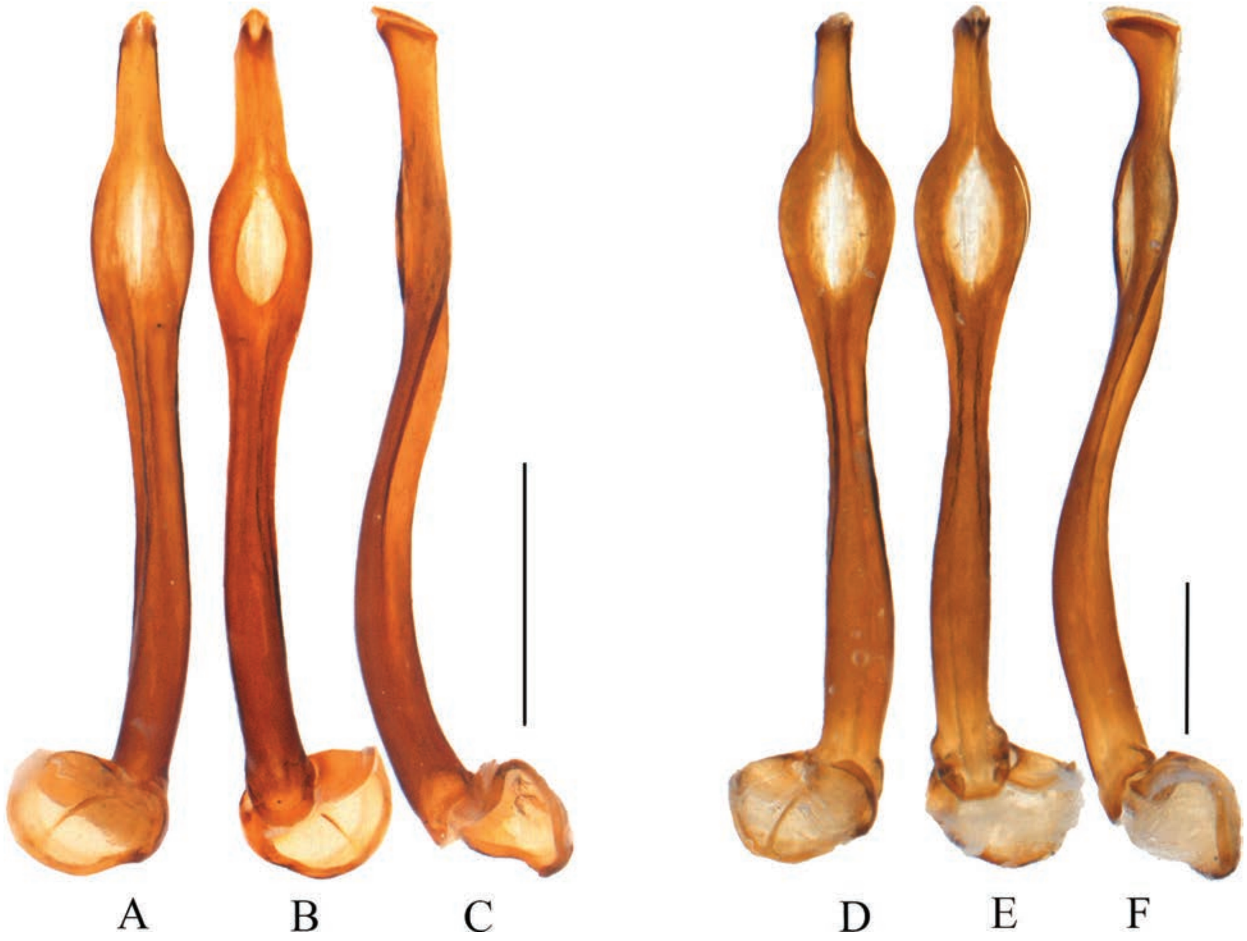


Figure 4. Aedeagi of *Macrolycus guangxiensis* Li, Bocak & Pang, 2015 (**A–C**) and *M. expansus* sp. nov. (**D–F**) **A, D** dorsal views **B, E** ventral views **C, F** lateral views. Scale bars: 1.0 mm.

Body black. Pronotum, elytra and scutellum dark red. Surface covered with decumbent red pubescence (Fig. 3B).

Eyes small, interocular distance about 1.6 times greater than eye diameter. Antennae flabellate, overlapping basal 2/3 length of elytra when inclined. Antennomeres III–XI lamellate; lamella of III 0.9 times as long as joint itself and rounded apically; lamellae of IV–XI pointed at apices, lamella of IX longest, 3.9 times longer than joint itself (Fig. 3B).

Pronotum square, 1.2 times wider than long. Anterior margin widely rounded and projecting anteriad, lateral margins feebly sinuate and posterior margin bisinuate; anterior angles confluent with anterior margin, posterior angles sharp and moderately projected. Scutellum trapezoidal, feebly emarginate at apex (Fig. 3B).

Elytra 3.9 times longer than humeral width. Costae I and III weak but visible along its length, IV as strong as II (Fig. 3B).

Phallus slender (Fig. 4D–F), basal part stout and distinctly narrowed towards middle in dorsal and ventral views (Fig. 4D, E), subapical part strongly and asymmetrically inflated laterally, about 2.8 times as wide as basal part, with an oval ventral-cavity, apical part nearly parallel-sided, apex with a deep V-shaped notch, about 0.19 times as wide as subapical part; basal 1/3 part stout and curved ventrally in lateral view (Fig. 4F), subapical part moderately inflated ventrally, apical part distinctly expanded ventrally, with a tapered lamella.

Distribution (Fig. 2). China (Zhejiang).

Macrolycus quartus Y. Yang, Du & Liu, sp. nov.

https://zoobank.org/809EBD56-644B-416A-B944-6A8E12A3F738
Figs 5A, B, 6A–C

Diagnosis. The species resembles *M. praecellens* Kazantsev, 1993, but can be distinguished from the latter by the following characters: lamellae of antennomeres III and IV obtuse at apices (Fig. 5A); phallus integrally stout (Fig. 6A–C), apical part relatively long and moderately expanded ventrally in lateral view (Fig. 6C). In contrast, in *M. praecellens*, lamellae of antennomeres III and IV are acute at apices (Kazantsev 1993: fig. 13); phallus is integrally slender, apical part is relatively short and strongly expanded ventrally in lateral view (Kazantsev 1993: fig. 12).

Figure 5. Habitus (dorsal views) of *Macrolycus quartus* sp. nov. (**A, B**) and *M. costus* sp. nov. (**C, D**) **A, C** males **B, D** females. Scale bars: 1.0 mm.

Etymology. The specific name is derived from the Latin *quartus* (the fourth), referring to its antennomere IV truncated at apex.

Type material. *Holotype*. China: ♂ (MHBU), Guangxi, Wuming, Damingshan, 1100 m, 27.v.2011, leg. H. Y. Liu. ***Paratypes*.** 3♂9♀ (MHBU), same data as the holotype; 3♂7♀ (MHBU), Guangxi, Wuming, Damingshan, 1230–1422 m, 20.v.2011, leg. H. Y. Liu.

Description. Male (Fig. 5A). Length 9.4–10.6 mm (10.0 mm in holotype), width at humeri 1.9–2.3 mm (2.2 mm in holotype).

Body black. Pronotum, elytra and scutellum dark red. Surface covered with decumbent red pubescence (Fig. 5A).

Eyes small, interocular distance about 2.3 times greater than eye diameter. Antennae flabellate, overlapping basal 2/3 length of elytra when inclined. Antennomere III triangular and obtuse apically, about 2.5 times longer than wide; IV–XI lamellate, lamella of IV apically obtuse and lamellae of V–XI pointed at apices; lamella of IX longest, 3.8 times longer than joint itself (Fig. 5A).

Pronotum square, 1.1 times wider than long. Anterior margin projecting anteriad and feebly emarginate at apex, lateral margins sinuate and posterior margin bisinuate; anterior angles rounded, posterior angles sharp and sharply projected. Scutellum trapezoidal, feebly emarginate at apex (Fig. 5A).

Elytra 3.8 times longer than humeral width. Costa I weak, II as strong as IV, and III weak and visible only at humeri (Fig. 5A).

Phallus slender (Fig. 6A–C), nearly parallel-sided basally in dorsal and ventral views (Fig. 6A, B), subapical part moderately and asymmetrically inflated laterally, about 1.89 times as wide as basal part, with an oval ventral-cavity, apical part progressively expanded distad, apex with a shallow V-shaped notch, about 0.54 times as wide as subapical part; basal 1/3 part feebly curved ventrally in lateral view (Fig. 6C), subapical part inflated ventrally, apical part moderately expanded ventrally, with a square lamella.

Female (Fig. 5B). Similar to male, but larger in body size. Length 11.5–13.9 mm, width at humeri 2.7–3.3 mm. Antennae serrate and shorter, overlapping elytral mid-length when inclined. Pronotum 1.2 times wider than long, anterior angles obtuse-angled.

Distribution (Fig. 2). China (Guangxi).

Macrolycus costus Y. Yang, Du & Liu, sp. nov.

https://zoobank.org/C4DA9323-4AE2-4625-872F-9FEC27E2B12E
Figs 5C, D, 6D–F

Diagnosis. The species resembles *M. guangxiensis*, but differs in the male antennae overlapping basal 2/3 length of elytra when inclined and a strong elytral costa III (Fig. 5C), phallus extremely slender at basal part in ventral view (Fig. 6D). Unlike in *M. guangxiensis*, the male antennae only reach elytral mid-length, elytral costa III is usually weak (Li et al. 2015: fig. 9), and phallus is relatively stout basally in ventral view (Li et al. 2015: fig. 29).

Etymology. The specific name is derived from the Latin *costa* (a rib), referring to its strong elytral costae III.

Type material. *Holotype*. China: ♂ (MHBU), Guangxi, Wuming, Damingshan, 1100 m, 27.v. 2011, leg. H. Y. Liu. ***Paratypes*.** 3♂4♀ (MHBU), same data as the holotype.

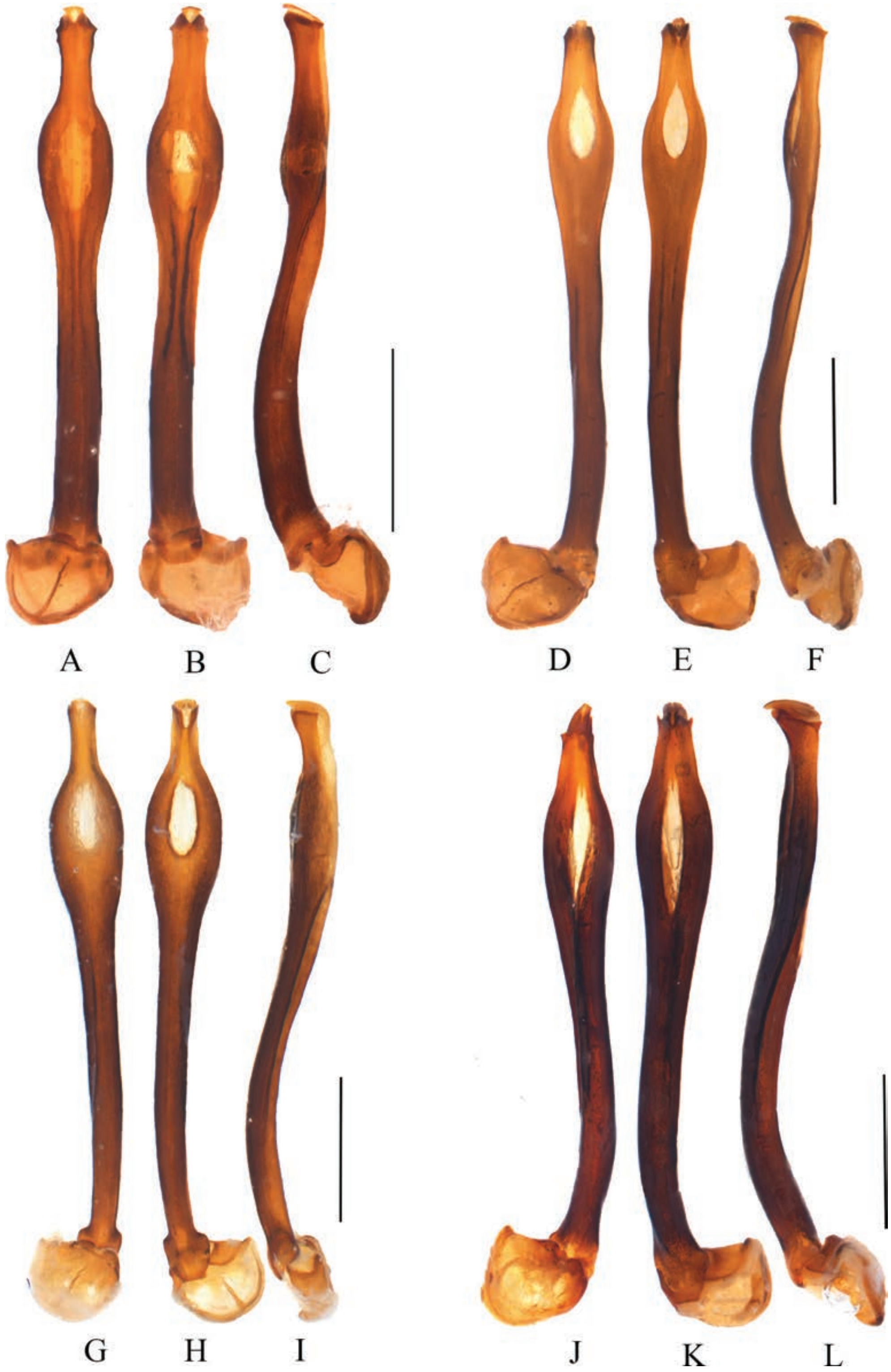


Figure 6. Aedeagi of *Macrolycus quartus* sp. nov. (**A–C**), *M. costus* sp. nov. (**D–F**), *M. opacipennis* sp. nov. (**G–I**) and *M. curtus* sp. nov. (**J–L**) **A, D, G, J** dorsal views **B, E, H, K** ventral views **C, F, I, L** lateral views. Scale bars: 1.0 mm.

Description. Male (Fig. 5C). Length 12.4 mm, width at humeri 2.8 mm.

Body black. Pronotum, elytra and scutellum red. Costae of elytra orange red. Surface covered with decumbent red pubescence (Fig. 5C).

Eyes small, interocular distance about 1.6 times greater than eye diameter. Antennae flabellate, overlapping basal 2/3 length of elytra when inclined. Antennomeres

III–XI lamellate, lamellae pointed at apices; lamella of III 0.6 times as long as joint itself; lamella of VIII longest, 4.2 times longer than joint itself (Fig. 5C).

Pronotum square, 1.1 times wider than long. Anterior margin widely rounded, lateral margins strongly sinuate and posterior margin bisinuate; anterior angles obtuse-angled, posterior angles sharp and moderately projected. Scutellum trapezoidal, straight at apex (Fig. 5C).

Elytra 3.6 times longer than humeral width. Costa I as strong as II, III and IV (Fig. 5C).

Phallus slender (Fig. 6D–F), basal part parallel-sided in dorsal and ventral views (Fig. 6D, E), subapical part strongly and asymmetrically inflated laterally, about twice as wide as basal part, with a fusiform ventral-cavity, apical part progressively narrowed distad, apex with a shallow V-shaped notch, about 0.46 times as wide as subapical part; basal 1/4 part curved ventrally in lateral view (Fig. 6F), subapical part moderately inflated ventrally, apical part moderately expanded ventrally, and with a tapered lamella.

Female (Fig. 6D). Similar to males, but larger in body size. Length 17.0–18.2 mm, width at humeri 4.0–4.5 mm. Antennae serrate and shorter, overlapping elytral mid-length when inclined. Pronotum 1.3 times wider than long, anterior angles obtuse-angled. Elytra 3.4 times longer than humeral width.

Distribution (Fig. 2). China (Guangxi).

Macrolycus opacipennis **Y. Yang, Du & Liu, sp. nov.**

https://zoobank.org/559D7E0F-0505-4958-A098-D8D381CD8480
Figs 6G–I, 7A, B

Diagnosis. This species differs from all others of the *M. ligulatus* species-group in the elytra darkened at costal intervals (Fig. 7A), while never darkened in others; basal part of phallus progressively widened towards middle in dorsal and ventral views (Fig. 6G, H), while narrowed towards middle or subparallel-sided in others.

Etymology. The specific name is derived from the Latin *opacus* (darkened, obscure) + *penna* (feather), referring to its elytra darkened at costal intervals.

Type material. ***Holotype***. China: ♂ (MHBU), Ningxia, Jingyuan, Wanghuanan, 3–4.vii.2009, leg. G. D. Ren & Y. B. Ba. ***Paratype.*** 1 ♀ (MHBU), same data as holotype.

Description. Male (Fig. 7A). Length 12.1 mm, width at humeri 2.7 mm.

Body black. Pronotum red with a square black patch in the center of the disc, elytra red and darkened at costal intervals, and scutellum red. Surface covered with decumbent red pubescence (Fig. 7A).

Eyes small, interocular distance about twice greater than eye diameter. Antennae flabellate, overlapping basal 2/3 length of elytra when inclined. Antennomere III with minute lamella, 0.6 times as long as joint itself and apically obtuse, IV–XI lamellate, lamellae pointed at apices; lamella of IX longest, 2.9 times longer than joint itself (Fig. 7A).

Pronotum square, 1.2 times wider than long. Anterior margin widely rounded, and feebly projecting anteriad, lateral margins sinuate and posterior margin straight; anterior angles rounded, posterior angles sharp and moderately projected. Scutellum trapezoidal, emarginate at apex (Fig. 7A).

Elytra 3.7 times longer than humeral width. Costae I and II as strong as IV, and III visible only basally (Fig. 7A).

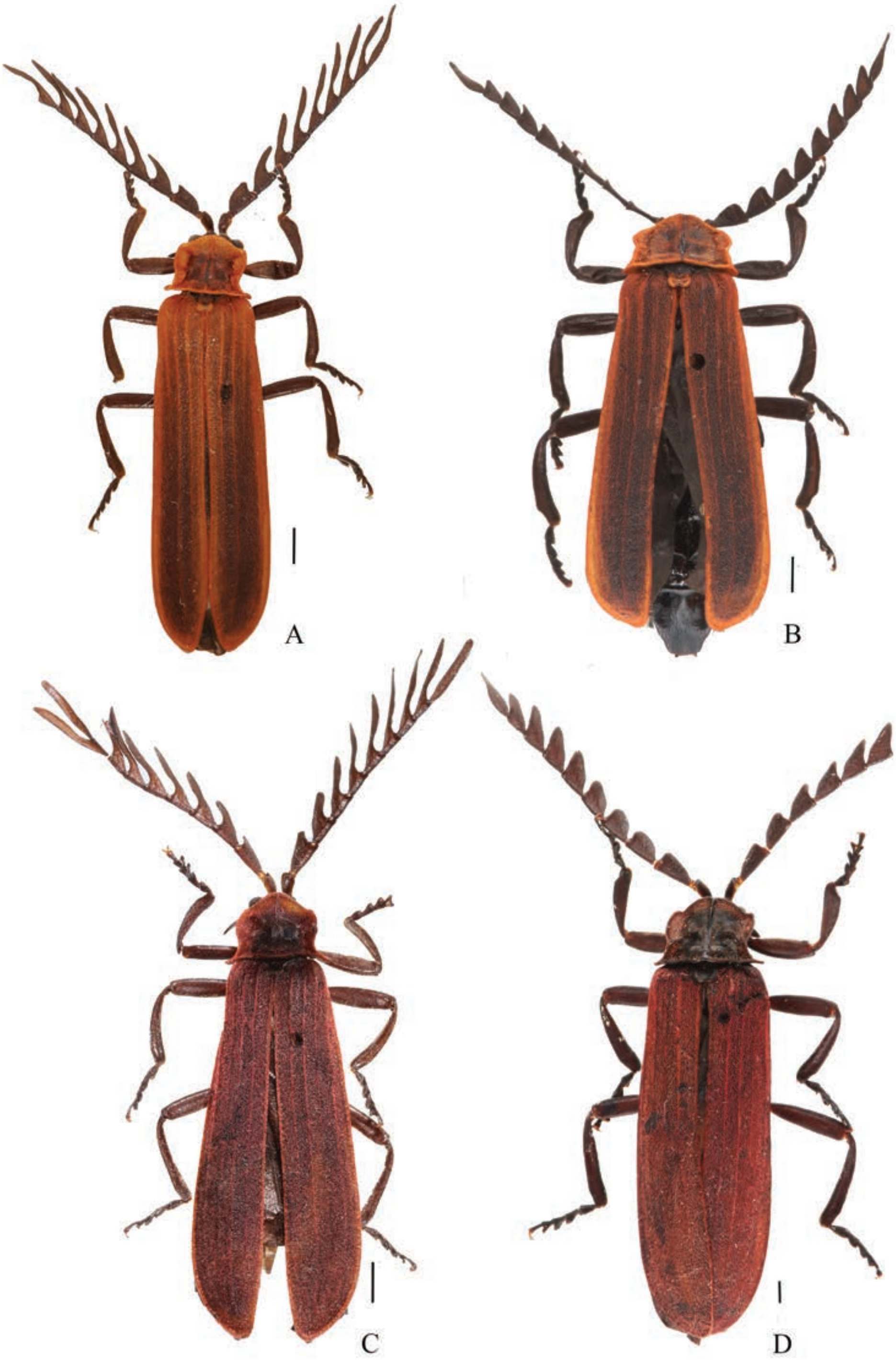


Figure 7. Habitus (dorsal views) of *Macrolycus opacipennis* sp. nov. (**A, B**) and *M. curtus* sp. nov. (**C, D**) **A, C** males **B, D** females. Scale bars: 1.0 mm.

Phallus slender (Fig. 6G–I), basal part progressively widened towards middle in dorsal and ventral views (Fig. 6G, H), subapical part strongly and asymmetrically inflated laterally, about 2.2 times as wide as basal part, with an oval ventral-cavity, apical part nearly parallel-sided, apex with a deep V-shaped notch, about 0.39 times as wide as subapical part; basal 1/4 part feebly curved ventrally in lateral view (Fig. 6I), subapical part feebly inflated ventrally, apical part moderately expanded ventrally, apex with a tapered lamella.

Female (Fig. 7B). Similar to male, but larger in body size. Length 13.0 mm, width at humeri 3.4 mm. Antennae serrate and shorter, overlapping basal 1/3 length of elytra when inclined. Pronotum 1.4 times wider than long. Elytra 3.0 times longer than humeral width, uncovering abdominal tergite VIII.

Distribution (Fig. 2). China (Ningxia).

Macrolycus curtus Y. Yang, Liu & X. Yang, sp. nov.

https://zoobank.org/D315E9DC-6731-4A7A-9578-927ED25DAD3D
Figs 6J–L, 7C, D

Diagnosis. The species resembles *M. costus* sp. nov. in the short apical part (1/10 length) and fusiform ventral-cavity of phallus, but differs in the weak elytral costa III (Fig. 7C) (strong in *M. costus* sp. nov.; Fig. 5C); phallus relatively stout and curved laterally at basal 1/4 portion in dorsal and ventral views (Fig. 6J–K) (slender and almost straight at basal part in dorsal and ventral views in *M. costus* sp. nov. (Fig. 6D–F).

Etymology. The specific name is derived from the Latin *curtus* (short), referring to the short apical part of its phallus.

Type material. *Holotype*. China: ♂ (IZAS), Gansu, Kangxian, Qinghe Forestry, 1400 m, 8.vii.1999, leg. J. Yao. ***Paratype***. 1 ♀ (IZAS), same data as holotype.

Description. Male (Fig. 7C). Length 11.5 mm, width at humeri 2.4 mm.

Body black. Pronotum dark red with a square black patch in the center of the disc, elytra and scutellum dark red. Surface covered with decumbent red pubescence (Fig. 7C).

Eyes small, interocular distance about 1.9 times greater than eye diameter. Antennae flabellate, overlapping basal 2/3 length of elytra when inclined. Antennomeres III–XI lamellate, lamellae of III and IV apically rounded and V–XI pointed at apices, lamella of III 0.6 times as long as joint itself, lamella of IX longest, 3.4 times longer than joint itself (Fig. 7C).

Pronotum square, 1.2 times wider than long. Anterior margin widely rounded, and feebly projecting anteriad, lateral margins sinuate and posterior margin almost straight; anterior angles rounded, posterior angles sharp and moderately projected. Scutellum trapezoidal, feebly emarginate at apex (Fig. 7C).

Elytra 4.0 times longer than humeral width. Costae I and II as strong as IV, and III visible only basally (Fig. 7C).

Phallus slender (Fig. 6J–L), basal part parallel-sided and curved laterally at basal 1/4 portion in dorsal and ventral views (Fig. 6J, K), subapical part moderately and asymmetrically inflated laterally, about 1.9 times as wide as basal part, with a fusiform ventral-cavity, apical part constricted distad, apex with a shallow V-shaped notch, about 0.47 times as wide as subapical part; basal 1/3 part moderately curved ventrally in lateral view (Fig. 6L), subapical part flat ventrally, apical part short and moderately expanded ventrally, with a tapered lamella.

Female (Fig. 7D). Similar to male, but larger in body size. Length 21.2 mm, width at humeri 5.4 mm. Antennae serrate and shorter, overlapping elytral mid-length when inclined. Pronotum 1.3 times wider than long. Elytra 3.3 times longer than humeral width.

Distribution (Fig. 2). China (Gansu).

Discussion

Li et al. (2015) divided the genus *Macrolycus* into nine species-groups based on a molecular phylogeny. The species-groups are generally defined by the shapes of apical part of the phallus and form of its attached structure. The *M. ligulatus* species-group can be distinguished from others by the phallus usually expanded ventrodistally, and present with a U- or V-shaped notch and a tongue-like lamella at the apex (Li et al. 2015). However, some species do not match the diagnosis very well, such as *M. chapaensis* and *M. extrusus*, whose apical parts of the phallus are expanded both ventrally and dorsally, similar to most species of the *M. murzini* species-group. Even more puzzling, some species were originally assigned to the *M. ligulatus* species-group, such as *M. parvus*, *M. bocakorum* and *M. notaticollis* (Li et al. 2015), but the apical parts of their phallus are feebly constricted distad in lateral view, corresponding with the diagnosis of the *M. venustus* species-group (Li et al. 2015). The morphological similarity between the *ligulatus* species-group and the *M. venustus* species-group has been noted by Li et al. (2015), but they were treated as separate groups because they belonged to different clades (although with lower supporting values) recovered in the molecular phylogeny. These individual species were considered to be a result of convergent evolution (Li et al. 2015). In this case, it is difficult to assign a species to the *M. ligulatus* species-group, *M. murzini* species-group or *M. murzini* species-group, if no molecular data is available. More samples or data are required to clarify the classification within *Macrolycus* in the future, which is beyond the scope of this study.

Nevertheless, the five new species discovered in the present study conform very well to the diagnosis of the *M. ligulatus* species-group and can be distinguished from others in the following key.

Key to world species of *Macrolycus ligulatus* species-group

1 Apical part of phallus expanded ventrally or both ventrally and dorsally in lateral view (e.g., Figs 4C, F, 6C, F, I, L; Kazantsev 1993: fig. 11; 2001: fig. 22; 2013: fig. 29; Li et al. 2012: fig. 33; 2015: fig. 28) **2**

– Apical part of phallus subparallel-sided or feebly constricted distad in lateral view (e.g., Kazantsev 2001: fig. 15; Li et al. 2015: fig. 30; Li 2015: fig. 11Q) **11**

2 Apical part of phallus expanded both dorsally and ventrally in lateral view (e.g., Kazantsev 2013: fig. 29; Li et al. 2012: fig. 31) **3**

– Apical part of phallus expanded only ventrally in lateral view (e.g., Figs 4C, F, 6C, F, I, L; Kazantsev 1993: fig. 11; 2001: fig. 22; Li et al. 2015: fig. 28) **4**

3 Apical part of phallus abruptly constricted at apical 1/10 portion then expanded distad in ventral view (Kazantsev 2013: fig. 28) .... ***M. chapaensis* Kazantsev, 2013**

– Apical part of phallus nearly parallel-sided in ventral view (Li et al. 2012: fig. 32) .... ***M. extrusus* Li, Bocak & Pang, 2012**

4 Antennomere III lamellate in male (e.g., Figs 3B, 5C, 7A, C; Li et al. 2015: fig. 9) **5**

– Antennomere III triangular in male (e.g., Fig. 5A; Kazantsev 1993: fig. 13; Li et al. 2012: fig. 48) **9**

5 Lamella of antennomere III as long as joint itself (Fig. 7C) ....***M. curtus* sp. nov.**

– Lamella of antennomere III at most 0.8 times as long as joint itself (e.g., Figs 3B, 5C, 7A; Li et al. 2015: fig. 9) **6**

6 Elytral costa III extremely strong (Fig. 5C); basal part of phallus relatively slender and parallel-sided in ventral view (Fig. 6F) .... ***M. costus* sp. nov.**

– Elytral costa III weak (e.g., Figs 3B, 7A; Li et al. 2015: fig. 9); basal part of phallus relatively stout or not parallel-sided in ventral view (e.g., Figs 4E, 6H; Li et al. 2015: fig. 29) **7**

7 Antennae shorter in males, at most extending to elytral mid-length when inclined (Li et al. 2015: fig. 9)........ ***M. guangxiensis* Li, Bocak & Pang, 2015**

– Antennae longer in males, at least reaching apical 2/3 length of elytra when inclined (e.g., Figs 5A, 7A)..**8**

8 Elytra uniformly dark red (Fig. 3B); basal part of phallus feebly narrowed towards middle in dorsal and ventral views (Fig. 4D, E) .... ***M. expansus* sp. nov.**

– Elytra darkened at costal intervals (Fig. 7A); basal part of phallus progressively widened towards middle in dorsal and ventral views (Fig. 6G, H) .... ***M. opacipennis* sp. nov.**

9 Lamellae of antennomeres III and IV obtuse at apices (Fig. 5A) ....***M. quartus* sp. nov.**

– Lamellae of antennomeres III and IV acute at apices (e.g., Kazantsev 1993: fig. 13; Li et al. 2012: fig. 48)..**10**

10 Phallus curved ventrally at basal 1/4 portion in lateral view, apical part short, about 1/12 length of phallus (Kazantsev 1993: fig. 12) .... ***M. praecellens* Kazantsev, 1993**

– Phallus curved ventrally at basal 1/3 portion in lateral view, apical part longer, about 1/6 length of phallus (Li et al. 2012: fig. 33) ....***M. ligulatus* Li, Bocak & Pang, 2012**

11 Body relatively small, less than 8.0 mm in length; interocular distance 2.1 times greater than eye diameter (Li et al. 2015: fig. 10) ....***M. parvus* Li, Bocak & Pang, 2015**

– Body relatively large, more than 10.0 mm in length; interocular distance at most 1.6 times greater than eye diameter..**12**

12 Basal part of phallus expanded in lateral view (Kazantsev 2001: fig. 15) ....***M. bocakorum* Kazantsev, 2001**

– Basal part of phallus never expanded in lateral view (Li 2015: fig. 11Q)....... ....***M. notaticollis* Pic, 1935**

Acknowledgments

We express our deep gratitude to the reviewers, Dr Oliver Keller and the other anonymous one, for their comments and corrections to our original manuscript. We also thank Dr Christopher Glasby for his linguistic edits on our manuscript.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

The present study was supported by the National Natural Science Foundation of China (Nos. 32270491, 31772507), the Natural Science Foundation of Hebei Province (No. C2022201005), and the Interdisciplinary Research Program of Natural Science of Hebei University (No. DXK202302).

Author contributions

Conceptualization, RLD, YXY, XKY, HYL. Data curation: RLD, YXY. Formal analysis: RLD, YXY. Methodology: RLD, YXY. Investigation: RLD, YXY, HYL. Visualization: RLD. Supervision: YXY, XKY, HYL. Writing—original draft preparation: RLD, YXY. Writinginal draft ting. WritRLD, YXY, XKY, HYL. All authors have read and agreed to the published version of the manuscript.

Author ORCIDs

Ruolan Du https://orcid.org/0009-0003-8774-4001
Yuxia Yang https://orcid.org/0000-0002-3118-6659
Xingke Yang https://orcid.org/0000-0003-3676-6828
Haoyu Liu https://orcid.org/0000-0003-1383-5560

Data availability

All of the data that support the findings of this study are available in the main text.

References

Du RL, Yang YX, Yang XK, Liu HY (2024) A taxonomic study on the nominate subgenus *Macrolycus* Waterhouse, 1878 from China (Coleoptera, Lycidae). Zootaxa 5424(3): 358–366. https://doi.org/10.11646/zootaxa.5424.3.4

Kazantsev SV (1993) Lycides nouveaux ou peu connus de l'Indochine (Coleoptera). Bulletin du Muséum National d'Histoire Naturelle 15(4): 49–68.

Kazantsev SV (2001) *Macrolycus* Waterhouse, 1878 (Coleoptera: Lycidae) of continental China. Elytron 14: 99–109.

Kazantsev SV (2002) New and little known species of Lycidae (Coleoptera) from China. Russian Entomological Journal 11: 253–263.

Kazantsev SV (2005) Morphology of Lycidae with some considerations on evolution of the Coleoptera. Elytron 19: 49–226.

Kazantsev SV (2013) New net-winged beetles (Coleoptera: Lycidae) from Indochina, with synonymic and taxonomic notes. Kavkazskij Entomologiceskij Bjulleten = Caucasian Entomological Bulletin 9(2): 247–252. https://doi.org/10.23885/1814-3326-2013-9-2-247-252

Kusy D, Motyka M, Bocek M, Masek M, Bocak L (2019) Phylogenomic analysis resolves the relationships among net-winged beetles (Coleoptera: Lycidae) and reveals the parallel evolution of morphological traits. Systematic Entomology 44(4): 911–925. https://doi.org/10.1111/syen.12363

Li Y (2015) Molecular phylogeny and taxonomy of the tribes Macrolycini and Lyponiini (Coleoptera: Lycidae). Masters thesis, Sun Yat-Sen University, Guangzhou, China (unpublished).

Li Y, Bocak L, Pang H (2012) New species of *Macrolycus* Waterhouse, 1878 from China and Laos, with a checklist of the genus (Coleoptera: Lycidae). Zootaxa 3232(1): 44–61. https://doi.org/10.11646/zootaxa.3232.1.2

Li Y, Bocak L, Pang H (2015) Molecular phylogeny of *Macrolycus* (Coleoptera: Lycidae) with description of new species from China. Entomological Science 18(3): 319–329. https://doi.org/10.1111/ens.12133

Liu HY, Du RL, Zhao W, Yang XK, Yang YX (2023) A morphometric approach to the comparative morphology of aedeagi shapes in net-winged beetles: A case study on the *Macrolycus dotatus* species group (Coleoptera: Lycidae). Arthropod Systematics & Phylogeny 81: 897–916.

Nakane T (1969) Lycidae (Insecta: Coleoptera). Fauna Japonica. Academic Press of Japan, Tokyo, [viii +] 224 pp. [8 pls]

Nakane T (1994) Revisional notes on the species of the genus *Macrolycus* Waterhouse in Japan (Insecta, Coleoptera, Lycidae). Biochemical Society Transactions 44: 3–9.

ZooKeys 1208: 331–346 (2024)
DOI: 10.3897/zookeys.1208.126092

Research Article

A new species of the newt genus *Hypselotriton* (Amphibia, Urodela, Salamandridae) from Jiangxi Province, southeastern China

Zhihao Jiang[1], Song Huang[1], Qiangyong Fan[2], Lin Cheng[2], Yanan Gong[1], Zhangbo Cui[1], Tierui Zhang[1], Wenjun Lan[2], Zhian Zou[2], Xuanzhi Huang[1], Jean Raffaëlli[3], Jinmin Chen[1]

1 *The Anhui Provincial Key Laboratory of Biodiversity Conservation and Ecological Security in the Yangtze River Basin, College of Life Sciences, Anhui Normal University, Wuhu 241000, China*
2 *Jiangxi Wuyishan National Nature Reserve Administration Bureau, Wuyishan National Nature Reserve, Shangrao, Jiangxi, China*
3 *Penclen, Plumelec, 56420, France*
Corresponding authors: Song Huang (snakeman@ahnu.edu.cn); Jinmin Chen (chenjinminkiz@126.com)

Abstract

A new newt species, *Hypselotriton huanggangensis* **sp. nov.**, is described based on nine specimens collected from Huanggangshan Mountains, Yanshan County, Jiangxi, China. Morphologically, the new species is characterized by the combination of nine external characters: (1) obvious black patches with clear boundaries on the whole body; (2) ground color of the dorsal body tan; (3) ground color of venter bright orange; (4) skin rough; (5) vertebral ridge weak; (6) fingers and toes overlapping when forelimb and hindlimb adpressed towards each other along body; (7) postocular orange spot absent; (8) small white warty glands around the eye; (9) two discontinuous longitudinal lines formed by white warty glands from neck to lateral parts of tail. Molecularly, the new species forms an independent clade with strong support in the phylogenetic trees of the genus based on the mitochondrial locus of NADH dehydrogenase subunit 2 (ND2) gene fragments. The new species distinctly differs from *H. fudingensis* by differences in its body measurements, vertebral ridge, dorsal black patches, and ventral black patches. Furthermore, the new species and *H. fudingensis* are geographically isolated by a series of high mountain ranges, including the Wuyishan and Jiufengshan Mountains. The number of *Hypselotriton* species is now 11.

Key words: Black patches, fire-bellied newts, geographical isolation, morphology, phylogenetics, taxonomy

Academic editor: Anthony Herrel
Received: 4 May 2024
Accepted: 2 July 2024
Published: 5 August 2024

ZooBank: https://zoobank.org/9B405A9D-B91D-43D3-89EE-CDC597A873EC

Citation: Jiang Z, Huang S, Fan Q, Cheng L, Gong Y, Cui Z, Zhang T, Lan W, Zou Z, Huang X, Raffaëlli J, Chen J (2024) A new species of the newt genus *Hypselotriton* (Amphibia, Urodela, Salamandridae) from Jiangxi Province, southeastern China. ZooKeys 1208: 331–346. https://doi.org/10.3897/zookeys.1208.126092

Introduction

The newt genus *Hypselotriton* Wolterstorff, 1934 (Urodela, Salamandridae) is distributed in China, including Anhui, Jiangsu, Zhejiang, Fujian, Jiangxi, Guangdong, Hubei, Henan, Hunan, Yunnan, and Guizhou Provinces (AmphibiaChina 2024; AmphibiaWeb 2024; Frost 2024). The generic classifications between *Hypselotriton* and *Cynops* has a lengthy history of taxonomic debate (Tschudi and Johann 1838; Wolterstorff 1934; Chang 1935; Zhao and Hu 1984; Zhao et al. 1988; Chan et al. 2001; Weisrock et al. 2006; Zhang et al. 2008; Dubois and Raffaëlli 2011, 2012; Raffaëlli 2013, 2022; Tominaga et al. 2013; Fei and

Ye 2016). Previously, some arrangements suggested that *Hypselotriton* is a junior synonym of *Cynops* (Ye et al. 1993; Wu et al. 2010a; Fei and Ye 2016). However, recent phylogenetic studies have presented evidence that *Cynops* sensu lato (including *Hypselotriton*) is paraphyletic with respect to *Pachytriton* and *Paramesotriton* (Rancilhac et al. 2021; Zhong et al. 2021; Yuan et al. 2022). Following the latest taxonomic arrangements (Dubois and Raffaëlli 2009; Dubois et al. 2021; Frost 2024) and the premise of monophyly, the genus *Cynops* Tschudi, 1838 is restricted to the Japanese species and all Chinese species are placed in the genus *Hypselotriton*.

Currently, the following 10 species of *Hypselotriton* have been recorded: *H. cyanurus* Liu, Hu & Yang, 1962; *H. yunnanensis* Yang, 1983; *H. chenggongensis* Kou & Xing, 1983; *H. wolterstorffi* Boulenger, 1905; *H. orientalis* David, 1873; *H. orphicus* Risch, 1983; *H. fudingensis* Wu, Wang, Jiang & Hanken, 2010; *H. maguae* Lyu, Qi & Wang, 2023; *H. jiaoren* Lyu, Qi & Wang, 2023; *H. glaucus* Yuan, Jiang, Ding, Zhang & Che, 2013. Recent studies suggest that overall species richness of *Hypselotriton* is underestimated (Yuan et al. 2022; Lyu et al. 2023). The reevaluations of the “widespread” species (*H. orientalis* and *H. yunnanensis*) and the survey of unexplored areas are likely to reveal overlooked diversity.

Huanggangshan Mountains (about 10 km long) is located on the northwestern side of the Wuyishan Mountains (about 550 km long), China. The highest peak (2161 m a.s.l) of Huanggangshan Mountains is known as the “roof of Eastern Mainland China” and “the first peak in the southeast of the mainland” (Lin and Ye 1985). During the recent surveys, on the northwestern side of the Huanggangshan Mountains, nine fire-bellied newts of unidentified *Hypselotriton* population were sampled in a small waterhole. After examination, they were found to differ from other congeneric members in both morphological and molecular characteristics. As a result, we herein describe it as a new species of *Hypselotriton*.

Materials and methods

Sampling

Nine specimens were collected in a small waterhole (28.15°N, 117.53°E; elevation 84 m) from Huanggangshan Mountains, Yanshan County, Shangrao City, Jiangxi (Fig. 1). The tiptoes of the specimens (the first toe of each specimen) were cut off and immediately preserved in 75% ethanol. These samples were then used for DNA analysis. After identifying that it is a new species, all fire-bellied newts were humanly euthanized by the injection of 0.7% tricaine methanesulfonate (MS222) solution (Yang et al. 2023), and fresh liver tissue was extracted and immediately preserved in 95% ethanol. The specimens were fixed in 10% formalin for one day, subsequently preserved in 75% ethanol and deposited in Anhui Normal University Museum (voucher numbers: HSA23097–23103, HSA23075–23076). Collections of all animals used for this present study obey the Wildlife Protection Act of China, following the guidelines and regulations approved by the internal review board of AHNU (approval no. AHNU-ET2023110), and with the permissions of local government authorities.

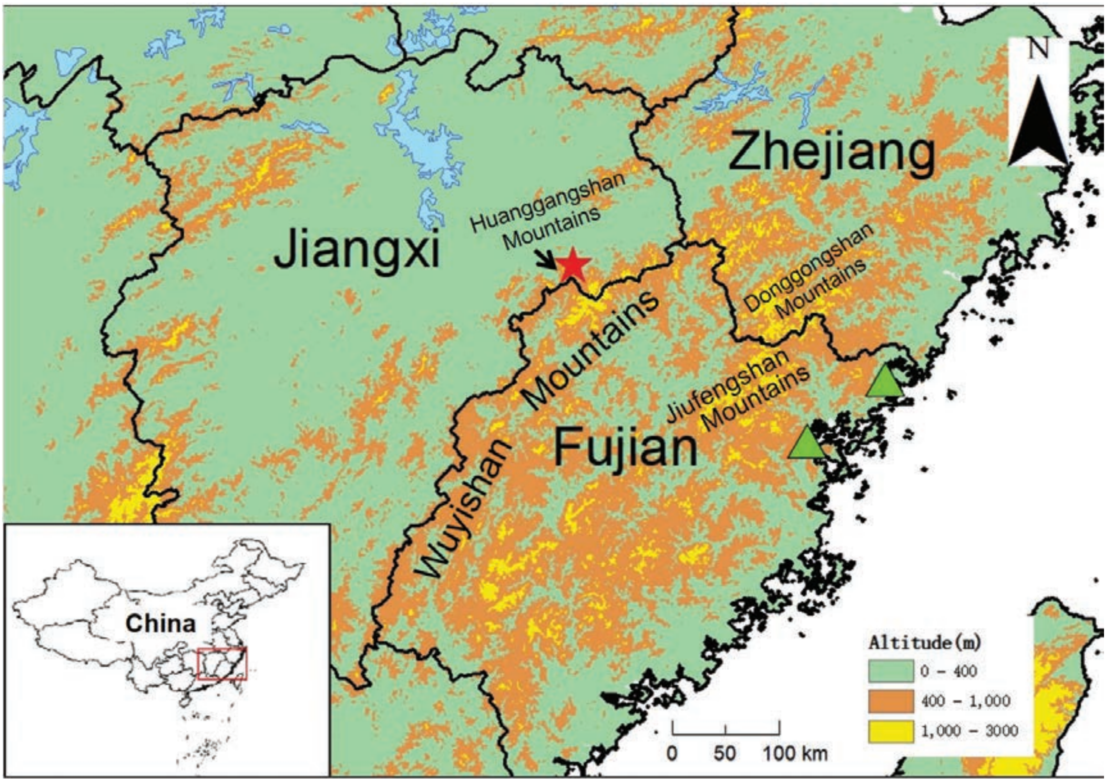


Figure 1. Geographic distribution of *Hypselotriton huanggangensis* sp. nov. (red star) and *H. fudingensis* (green triangles) in southeastern China. They are separated by the Wuyishan and Jiufengshan Mountains.

Morphological examination

External measurements were made for the seven specimens of *H. huanggangensis* sp. nov. and nine specimens of *H. fudingensis* with digital calipers to the nearest 0.1 mm. Only adult specimens were measured (Lyu et al. 2023). These 14 measurements are as follows: total length (TOL) from tip of snout to tip of tail; snout–vent length (SVL) from tip of snout to posterior edge of vent; tail length (TAL) from posterior edge of vent to tip of tail; maximum tail depth (TAD); head length (HL) from tip of snout to the posterior edge of the parotoid gland; maximum head width (HW); snout length (SL) from tip of snout to the anterior corner of eye; eye diameter (ED) from the anterior corner to the posterior corner of the eye; interorbital distance (IOD) between the anterior corner of each eye; eye–nostril length (EN) from the anterior corner of the eye to the nostril; internasal distance (IND) between the external nares; axilla–groin length (AG) between the axilla and the groin along the body; forelimb length (FLL) from elbow to tip of finger III; and hindlimb length (HLL) from knee to tip of toe III.

Statistical analyses on the morphometric measurements were performed in IBM SPSS Statistics 27.0. Males and females were analyzed separately, due to obvious sexual size dimorphism (Fei et al. 1990, 2006, 2012; Fei and Ye 2016). All measurements were made to normalize and reduce the variance (most *P* values > 0.05 in the Levene's test). Univariate Analysis of Covariance (ANCOVA) with SVL as the covariate were used to test for differences between *H. huanggangensis* sp. nov. and *H. fudingensis* (Lai & Lue, 2008).

Molecular phylogeny

Total genomic DNA was extracted from ethanol-preserved liver tissues, using the Qiagen DNEasy blood and tissue extraction kit (Qiagen Inc., Valencia, CA, USA). The phylogenetic relationships within *Hypselotriton* were derived from an analysis of the mtDNA fragment that codes for subunit two of NADH dehydrogenase (ND2) and its flanking tRNAs. A 1026-bp fragment was amplified using primers KIZL4437 (Yuan et al. 2011) and 5081R (Wu et al. 2010b). Two internal primers ND2–38R (5'–TATTCAYCCTAARTGTGCR–3') and 4416F (Wu et al. 2010b) were applied for sequencing (Yuan et al. 2013). Standard polymerase chain reactions (PCR) were performed in a final volume of 15 ul with the following procedures: initial denaturation at 94 °C for 5 min, 35 amplification cycles at 94 °C for 1 min, annealing for 1 min at 52 °C, extension for 1 min at 72 °C. Final extension at 72 °C was conducted for 10 min. The successfully amplified products were purified using ExoSAP-IT purification kit according to the manufacturer's instruction (Yuan et al. 2013). Purified PCR products were directly sequenced in both directions using a BigDye Terminator Cycle Sequencing Kit (v. 2.0, Applied Biosystems, Foster City, California, USA) and an ABI PRISM 3730 automated DNA sequencer (Yuan et al. 2013). For the phylogenetic analyses, 38 sequences from additional Chinese *Hypselotriton* congeners and two sequences of outgroup species of the genera *Pachytriton* Boulenger, 1878 and *Paramesotriton* Chang, 1935, were obtained from GenBank and incorporated into our dataset. Detailed information is provided in Table 1 (ID means the ordinal numbers of the species). DNA sequences were aligned using MEGA v. 6.0.6 (Kumar et al. 2018) with default parameters and manually checked.

Table 1. Localities, voucher information (Holotype: HSA23097), and GenBank accession numbers for all samples of ND2 used in this study.

ID	Species	Localities	Voucher	ND2
1	*Hypselotriton huanggangensis* sp. nov.	China: Jiangxi: Shangrao: Yanshan	HSA23075	PP590780
2	*Hypselotriton huanggangensis* sp. nov.	China: Jiangxi: Shangrao: Yanshan	HSA23076	PP590788
3	*Hypselotriton huanggangensis* sp. nov.	China: Jiangxi: Shangrao: Yanshan	HSA23097	PP590781
4	*Hypselotriton huanggangensis* sp. nov.	China: Jiangxi: Shangrao: Yanshan	HSA23098	PP590782
5	*Hypselotriton huanggangensis* sp. nov.	China: Jiangxi: Shangrao: Yanshan	HSA23099	PP590783
6	*Hypselotriton huanggangensis* sp. nov.	China: Jiangxi: Shangrao: Yanshan	HSA23100	PP590784
7	*Hypselotriton huanggangensis* sp. nov.	China: Jiangxi: Shangrao: Yanshan	HSA23101	PP590785
8	*Hypselotriton huanggangensis* sp. nov.	China: Jiangxi: Shangrao: Yanshan	HSA23102	PP590786
9	*Hypselotriton huanggangensis* sp. nov.	China: Jiangxi: Shangrao: Yanshan	HSA23103	PP590787
10	*Hypselotriton orientalis*	China: Anhui: Huangshan: Furonggu	SYS a002711	OQ116690
11	*Hypselotriton orientalis*	China: Anhui: Huoshan: Shangtushi	KIZ 021844	ON793742
12	*Hypselotriton orientalis*	China: Anhui: Xiuning: Dafu	KIZ 021962	ON793737
13	*Hypselotriton orientalis*	China: Henan: Xinyang: Mt Jigong	KIZ 013021	ON793736
14	*Hypselotriton orientalis*	China: Jiangxi: Jiujiang	KIZ 020539	ON793739
15	*Hypselotriton orientalis*	China: Jiangxi: Shangrao: Wannian	CIB 97867	GU301788
16	*Hypselotriton orientalis*	China: Jiangxi: Shangrao: Wuyuan	KIZ YPX25002	ON793740
17	*Hypselotriton orientalis*	China: Zhejiang: Jinhua	KIZ 06358	ON793718
18	*Hypselotriton orientalis*	China: Zhejiang: Quzhou	CIB 97919	GU301790

ID	Species	Localities	Voucher	ND2
19	*Hypselotriton orientalis*	China: Zhejiang: Taizhou: Tiantai	KIZ 012941	ON793732
20	*Hypselotriton fudingensis*	China: Fujian: Ningde: Mt Taimu	CIB 97874	GU301785
21	*Hypselotriton fudingensis*	China: Fujian: Ningde: Jiulongjing	SYS a008487	OQ116688
22	*Hypselotriton fudingensis*	China: Fujian: Ningde: Jiulongjing	SYS a008488	OQ116689
23	*Hypselotriton fudingensis*	China: Fujian: Ningde: Qingyu	KIZ 012214	ON793743
24	*Hypselotriton glaucus*	China: Guangdong: Meizhou: Mianyang	KIZ 09793	ON793715
25	*Hypselotriton glaucus*	China: Guangdong: Meizhou: Mianyang	KIZ 09799	ON793716
26	*Hypselotriton glaucus*	China: Guangdong: Meizhou: Mianyang	KIZ 09800	ON793717
27	*Hypselotriton orphicus*	China: Fujian: Fuzhou: Yongtai	KIZ 09905	ON793728
28	*Hypselotriton orphicus*	China: Fujian: Quanzhou: Mt Daiyun	KIZ 09839	ON793723
29	*Hypselotriton orphicus*	China: Guangdong: Chaozou	KIZ 09816	ON793719
30	*Hypselotriton jiaoren*	China: Guangdong: Qingyuan: Yingde	SYS a008786	OQ116679
31	*Hypselotriton jiaoren*	China: Guangdong: Qingyuan: Yingde	SYS a008787	OQ116680
32	*Hypselotriton jiaoren*	China: Guangdong: Qingyuan: Yingde	SYS a008788	OQ116681
33	*Hypselotriton jiaoren*	China: Guangdong: Qingyuan: Yingde	SYS a008789	OQ116682
34	*Hypselotriton jiaoren*	China: Guangdong: Qingyuan: Yingde	CIB 118534	OQ116683
35	*Hypselotriton jiaoren*	China: Guangdong: Qingyuan: Yingde	SYS a008791	OQ116684
36	*Hypselotriton maguae*	China: Jiangxi: Fuzhou: Mt Magu	CIB 118535	OQ116685
37	*Hypselotriton maguae*	China: Jiangxi: Fuzhou: Mt Magu	SYS a007032	OQ116686
38	*Hypselotriton cyanurus*	China: Guizhou: Liupanshui: Shuicheng	CIB 95897	GU301784
39	*Hypselotriton cyanurus*	China: Guizhou: Liupanshui: Shuicheng	KIZ 02331	ON793754
40	*Hypselotriton cyanurus*	China: Guizhou: Liupanshui: Shuicheng	KIZ 02332	ON793755
41	*Hypselotriton yunnanensis*	China: Yunnan: Chuxiong: Zijing	KIZ 021922	ON793749
42	*Hypselotriton yunnanensis*	China: Yunnan: Chuxiong: Zijing	KIZ 021923	ON793750
43	*Hypselotriton yunnanensis*	China: Yunnan: Kunming: Gulu	KIZ 022160	ON793752
44	*Hypselotriton yunnanensis*	China: Yunnan: Kunming: Huahongdong	KIZ 022157	ON793751
45	*Hypselotriton yunnanensis*	China: Yunnan: Pu'er: Ning'er	KIZ 01445	ON793756
46	*Hypselotriton yunnanensis*	China: Yunnan: Pu'er: Ning'er	KIZ 03900	ON793747
47	*Hypselotriton yunnanensis*	China: Yunnan: Pu'er: Ning'er	KIZ 03901	ON793748
48	*Pachytriton archospotus*	China: Hunan: Guidong	KIZ 04563	KU375007
49	*Paramesotriton chinensis*	China: Zhejiang: Jinhua:Panan	KIZ 06335	KU375034

The matrilineal genealogy was reconstructed using Bayesian-inference (BI) and maximum-likelihood (ML) methods based on ND2 gene. PartitionFinder2 was used to test the best partitioning scheme and jModelTest v. 2.1.2 was used to test the best fitting nucleotide substitution model. The data were analyzed using BI in MrBayes v. 3.2.4 (Ronquist et al. 2012), and ML in RaxmlGUI v. 1.3 (Silvestro and Michalak 2012). Two independent runs were conducted in a BI analysis, each of which was performed for 10 million generations and sampled every 1000 generations with the first 25% samples discarded as burn-in, resulting in a potential scale reduction factor (PSRF) of <0.005. The analyses used the proportion of invariable sites estimated from the data and 1000 bootstrap pseudoreplicates under the GTR+gamma model (Chen et al. 2021). Nodes in the trees were considered well supported when Bayesian posterior probabilities (BPP) were ≥ 0.95 and ML bootstrap support (BS) was ≥ 70% (Chen et al. 2021). Mean genetic distances between and within species were calculated in MEGA v. 6.0.6 using the uncorrected genetic distance (*p*-distances) model.

Results

Morphologically, our newly collected specimens can be distinguished from all known congeners (details in the taxonomic account below), which can be reliably identified by the obvious black patches with clear boundaries on the whole body and weak vertebral ridge. Statistical analyses on the morphometric measurements were performed on the specimens from northeastern Jiangxi and its sister species *H. fudingensis* from northeastern Fujian (Table 2). The results of *T*-test on morphometrics showed that individuals of the northeastern Jiangxi population and *H. fudingensis* are obviously different in HL, ED, and IND for males (p-values < 0.05), and in TAD for females (p-values < 0.05). Furthermore, once differences attributable to SVL were accounted for (Table 4), there were significant differences between *H. huanggangensis* sp. nov. and *H. fudingensis* for TAD, HL, ED, and AG in males, and significant differences for TOL, TAD, HL, HW, AG, FLL and HLL in females.

BI and ML analyses resulted in similar identical topologies (Fig. 2). As shown in the tree (Fig. 2), three major clades with strong support were revealed for the samples of *Hypselotriton*, while the relationship among these clades are not resolved. The first clade is composed of samples of *H. cyanurus* (BPP 1.00, BS 100) and *H. yunnanensis* (BPP 1.00, BS 97). The second clade consists of *H. glaucus* from eastern Guangdong (BPP 1.00, BS 100) and *H. jiaoren* from northern Guangdong (BPP 1.00, BS 100). In the third clade, the new specimens from northeastern Jiangxi form a distinct lineage (BPP 1.00, BS 100), which is sister to *H. fudingensis* with support values (BPP 1.00, BS 99). The genetic distances based on the ND2 gene among species of *Hypselotriton* are presented in Table 3. The putative new species from Huanggangshan Mountains showed obvious genetic divergence from other congeners. When compared with closely related recognized congeners, the minimum uncorrected genetic distance was 2.2% between the clade from Huanggangshan Mountains and *H. fudingensis* (Table 3).

Accordingly, combining the results of the morphological examination presented below and the phylogenetic analysis, the specimens from northeastern Jiangxi are regarded as a new species that is described herein.

Table 2. Morphometric comparisons based on the morphometric measurements (in mm) of *Hypselotriton huanggangensis* sp. nov. and *H. fudingensis*. * p-values < 0.05, ** p-values < 0.01.

	Holotype	***H. huanggangensis* sp. nov.**		***H. fudingensis***		***P*-values**	
	HSR23097	**Male (*n* = 5)**	**Female (*n* = 2)**	**Male (*n* = 2)**	**Female (*n* = 7)**	**Males**	**Females**
TOL	75.14	73.0–79.1 (74.8±2.5)	79.6–89.4	69.4–77.7	81.1–101.0 (90.8±6.6)	0.691	0.277
SVL	45.62	42.9–47.3 (44.9±1.7)	44.4–51.1	42.9–45.8	46.5–54.5 (51.0±3.3)	0.754	0.314
TAL	30.35	29.0–33.0 (30.8±1.5)	36.1–38.7	28.8–31.6	36.1–49.0 (40.7±4.4)	0.669	0.263
TAD	7.08	6.7–7.4 (7.0±0.3)	7.4–8.4	5.1–6.2	5.5–7.4 (6.4±0.6)	0.224	0.045*
HL	13.6	12.6–13.6 (13.0±0.4)	12.0–14.4	11.7–12.5	13.2–15.5 (14.1±0.7)	0.040*	0.298
HW	9.16	8.7–9.5 (9.1±0.3)	9.0–10.4	8.3–8.8	8.9–10.5 (9.8±0.5)	0.084	0.878
SL	3.98	4.0–4.4 (4.2±0.2)	3.5–4.6	4.2–4.4	4.1–4.9 (4.4±0.3)	0.472	0.645
ED	3.63	3.5–3.7 (3.6±0.1)	3.7–4.3	3.2–3.3	3.1–4.0 (3.5±0.3)	0.003**	0.202
IOD	5.37	5.0–5.4 (5.3±0.2)	4.9–5.2	4.4–5.3	4.8–5.8 (5.4±0.3)	0.507	0.333
EN	2.86	2.9–3.2 (3.0±0.1)	2.6–3.5	2.9–3.1	2.6–3.3 (3.1±0.2)	0.809	0.914
IND	2.77	2.4–2.8 (2.5±0.2)	2.6–2.9	1.9–2.1	1.9–3.8 (2.5±0.6)	0.021*	0.668
AG	20.19	18.4–21.4 (19.8±1.1)	21.5–24.5	18.2–19.7	20.8–26.1 (24.2±1.9)	0.386	0.659
FLL	12.28	12.3–14.5 (13.4±1.0)	13.6–15.2	12.9–14.2	13.3–15.2 (14.2±0.8)	0.807	0.780
HLL	13.95	14.0–16.2 (15.0±1.0)	13.8–17.2	14.0–14.4	13.5–16.3 (14.9±1.1)	0.188	0.878

Table 3. Uncorrected *p*-distances (%) based on the ND2 gene among *Hypselotriton* species (in 0.1%).

ID	Species	1	2	3	4	5	6	7	8	9
1	*Hypselotriton huanggangensis* sp. nov.	0								
2	*Hypselotriton orientalis*	7.2	2.7							
3	*Hypselotriton fudingensis*	2.2	8.0	0.5						
4	*Hypselotriton glaucus*	18.8	19.6	18.7	0.5					
5	*Hypselotriton orphicus*	11.8	14.0	12.3	19.9	2.0				
6	*Hypselotriton jiaoren*	18.3	19.5	17.8	6.6	19.3	0.6			
7	*Hypselotriton maguae*	13.9	13.8	13.3	22.5	13.2	21.3	0		
8	*Hypselotriton cyanurus*	21.1	21.3	20.6	20.8	20.8	19.5	23.4	0	
9	*Hypselotriton yunnanensis*	19.6	20.4	20.0	20.9	20.8	20.9	22.8	11.5	2.6

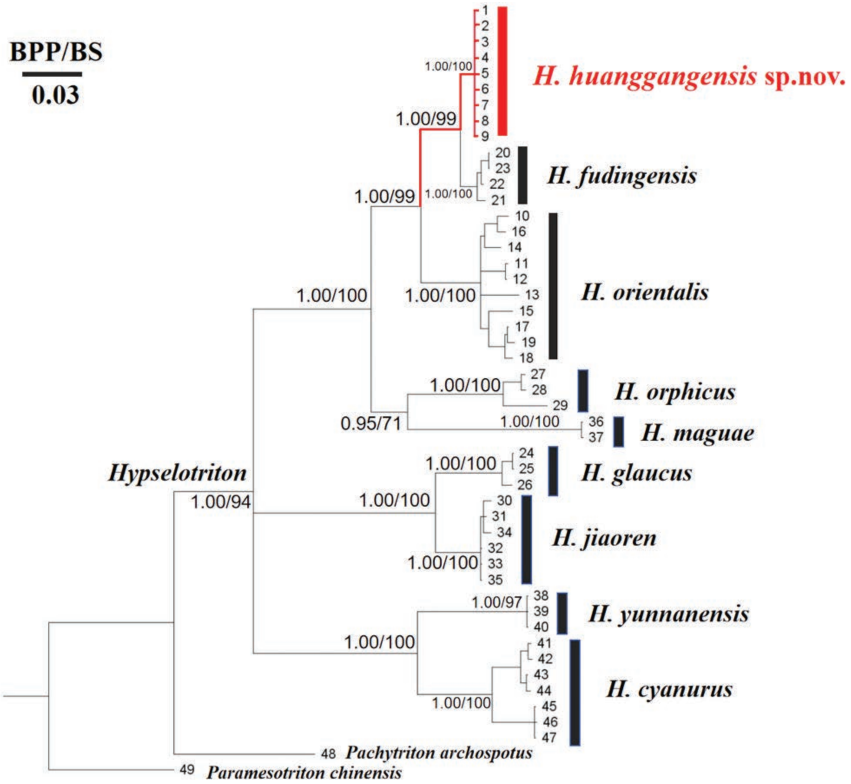


Figure 2. Bayesian-inference tree and maximum-likelihood phylogenies based on mitochondrial ND2 gene. Bayesian posterior probabilities and the bootstrap supports (BPP/BS) are shown near the notes. Number at the ends of the lineages correspond to the IDs in Table 1.

Taxonomic account

Hypselotriton huanggangensis **Jiang, Huang, Fan, Cheng, Raffaëlli & Chen, sp. nov.**
https://zoobank.org/18334E5C-BED9-47AE-A42D-FA916E7B2CC2
Figs 3–5

Type material. ***Holotype*.** HSA 23097, adult male from Huanggangshan Mountains (28.72°N, 117.33°E; elevation 84 m), Yanshan County, Shangrao City, Jiangxi Province, China, collected by Zhihao JIANG on 22 July 2023.

Paratypes. Six adult males: HSA23075–23076, HSA23098–23099, HSA23102–23103, and two adult females: HSA23100–23101. Same collection date and locality as the holotype.

Etymology. The specific name *huanggangensis* refers to the type locality in the Huanggangshan Mountains. For the English common name, we suggest "Huanggangshan Fire-bellied Newt" and for the Chinese name, 黄岗山蝾螈 (huáng gǎng shān róng yuán).

Diagnosis. (1) Small body size, TOL 73.0–79.1 mm in adult males, TOL 79.6–89.4 mm in adult females; (2) obvious black patches with clear boundaries on the whole body; (3) ground color of the dorsal body tan; (4) skin rough; (5) ground color of venter bright orange; (6) vertebral ridge weak; (7) fingers and toes overlapping when forelimb and hindlimb adpressed towards each other along body; (8) parotoid gland inconspicuous; (9) postocular orange spot absent; (10) white warty glands around the eye; (11) two discontinuous longitudinal lines which consist of white warty glands from neck to lateral parts of tail (Fig. 6).

Description of the holotype. HSA 23097 (Figs 4, 5), adult male with a small, slender body (TOL 79.1 mm, SVL 47.3 mm). Head oval in dorsal view; snout truncate, projecting slightly beyond mandible; nostril small but conspicuous; tongue elongate, enlarged anteriorly, with free lateral margin; vomerine tooth patch ∧–shaped; parotoid gland inconspicuous, gill remnants absent; gular fold present; skin with fine granules, covering most parts of dorsum, venter, chin and tail; vertebral ridge weak; cloacal opening oval, slightly protruding; limbs slender, fingers and toes overlapping when forelimb and hindlimb adpressed towards each other along the body; four fingers and five toes, slender and elongated, lacking webbing; relative length of fingers I < IV < II < III; relative length of toes I < V < II < IV < III. Tail laterally compressed, tapers posteriorly; caudal fin distinct; tail tip bluntly pointed.

Figure 3. Paratypes of *Hypselotriton huanggangensis* sp. nov. (HSA23075) **A** dorsalateral view in life **B** ventral view in life **C** small waterhole around mountain shrubs without direct sunlight at the type locality.

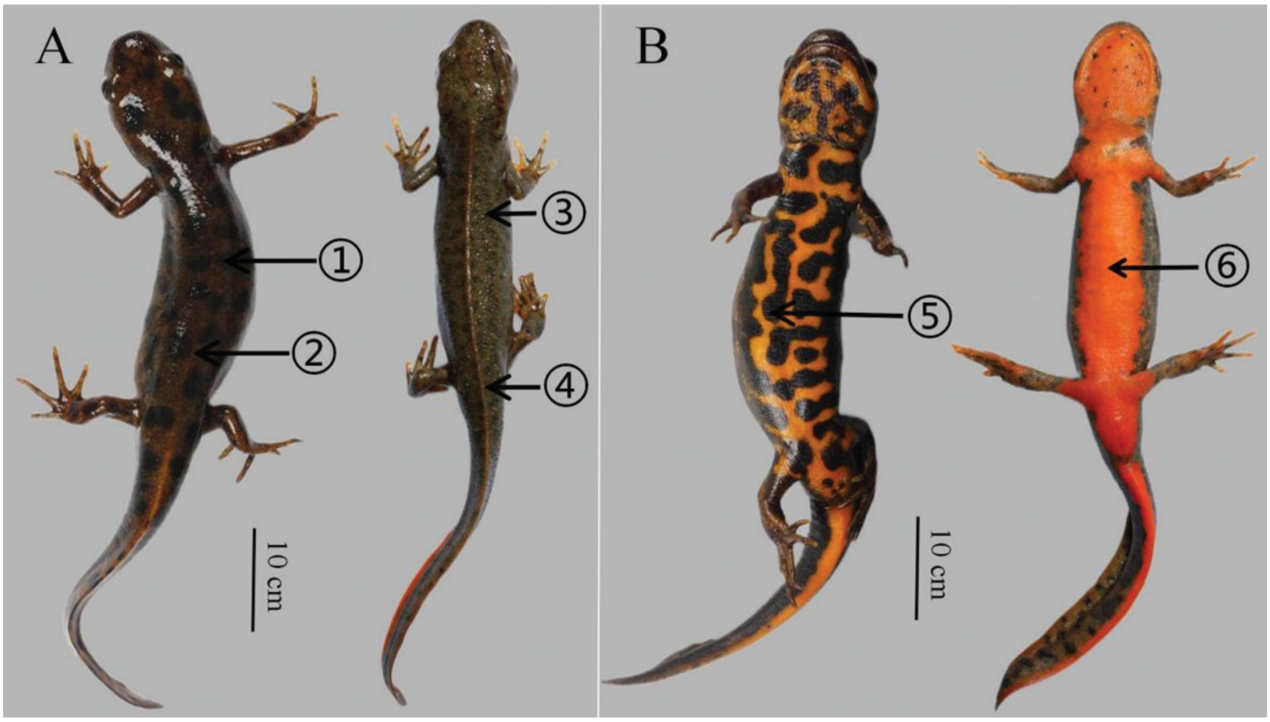


Figure 4. Comparison of holotype of *Hypselotriton huanggangensis* sp. nov. (left, HSA23097) and *Hypselotriton fudingensis* (right, HSA23108) in life **A** dorsal view **B** ventral view, 1, 5 obvious black patches, 2 weak vertebral ridge, 3 small spots, 4 conspicuous vertebral ridge, 6 bright orange venter without dark blotches.

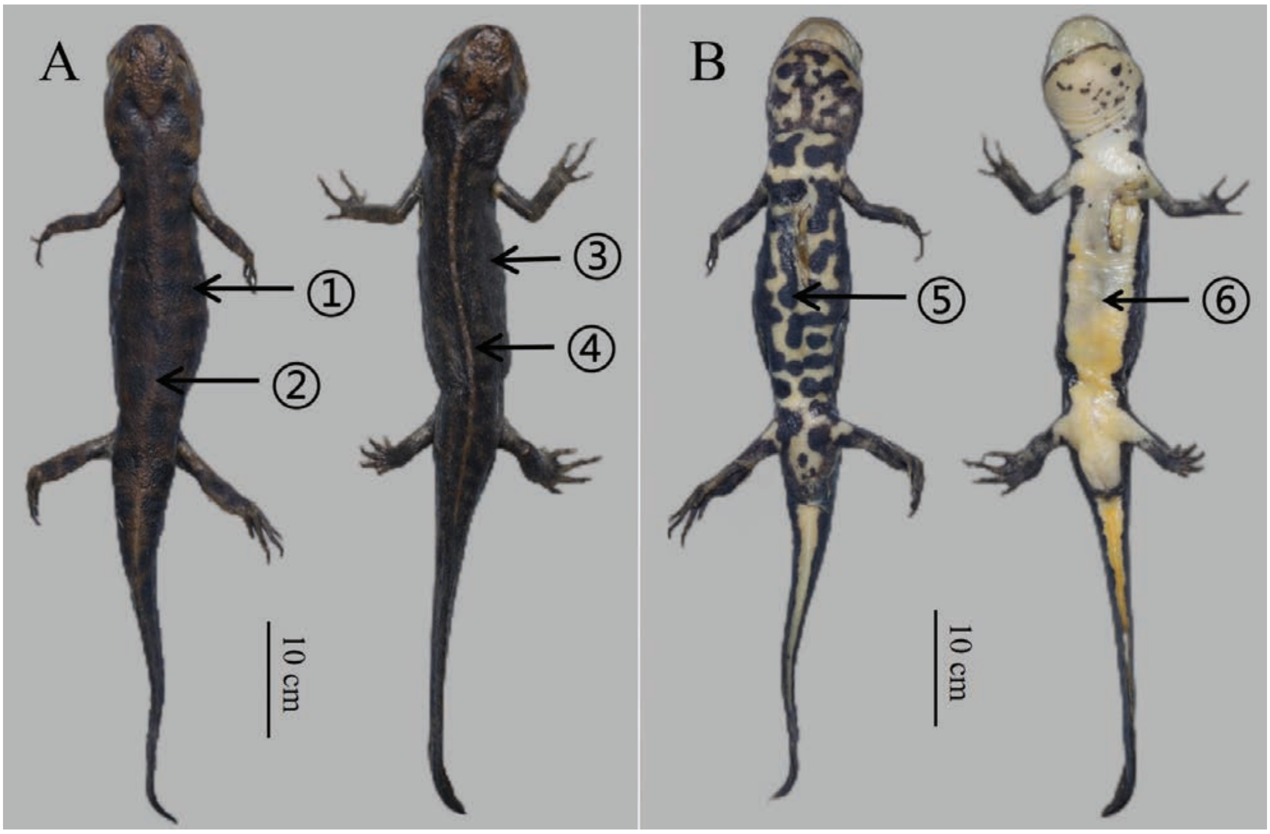


Figure 5. Comparison of holotype of *Hypselotriton huanggangensis* sp. nov. (left, HSA23097) and *Hypselotriton fudingensis* (right, HSA23104) in preservative **A** dorsal views **B** ventral views, 1–6 same as in Fig. 4.

Table 4. Test for differences between *H. huanggangensis* sp. nov. and *H. fudingensis* using ANCOVA (SVL as covariate).

Variable	Males	Females
Total length (TOL)		
F	6.78	12.17
P	0.052	0.008
Tail length (TAL)		
F	1.09	2.27
P	0.419	0.185
Maximum tail depth (TAD)		
F	12.34	15.48
P	0.019	0.004
Head length (HL)		
F	8.76	9.66
P	0.035	0.013
Maximum head width (HW)		
F	3.77	16.71
P	0.120	0.004
Snout length (SL)		
F	1.18	1.23
P	0.395	0.357
Eye diameter (ED)		
F	12.00	1.91
P	0.020	0.228
Interorbital distance (IOD)		
F	1.20	1.48
P	0.390	0.301
Eye–nostril length (EN)		
F	0.03	0.38
P	0.967	0.700
Internasal distance (IND)		
F	5.91	0.189
P	0.064	0.833
Axilla–groin length (AG)		
F	76.89	9.38
P	0.010	0.014
Forelimb length (FLL)		
F	0.07	8.86
P	0.938	0.016
Hindlimb length (HLL)		
F	1.48	5.65
P	0.330	0.042

Coloration of the holotype. In life, obvious black patches with clear boundaries on the whole body; ground color of the dorsal body tan; ground color of venter bright orange; white warty glands from the lateral part of head to tail; axilla, cloacal opening, and venter of tail bright orange. In preservative after six months (Fig. 5), dorsum, flanks, and limbs slightly darker. All orange coloration of venter fades to creamy white.

Figure 6. Two discontinuous longitudinal lines which consist of white warty glands from neck to lateral parts of tail (*Hypselotriton huanggangensis* sp. nov., HSA23099) in life.

Variation. Linear measurements are summarized in Table 2. Females (TOL 79.6–89.4 mm) are distinctly larger than males (TOL 73.0–79.1 mm). All paratypes resemble the holotype except that the cloaca is wider and more swollen in males than in females, the irregular bright-orange patches on ventral surface occupy more surface in females than in males, and the gular fold absent in some individuals.

Comparisons. *Hypselotriton huanggangensis* sp. nov. is phylogenetically close to *H. fudingensis*, which is distributed in northeastern Fujian. However, *H. huanggangensis* sp. nov. differs from *H. fudingensis* by its weak vertebral ridge (vs vertebral ridge conspicuous), dorsal black patches (vs small or no spots on dorsum), and ventral black patches (vs venter bright orange without dark blotches).

In addition, *H. huanggangensis* sp. nov. further differs from the remaining congeners.

Hypselotriton huanggangensis sp. nov. differs from *H. orphicus* by its weak vertebral ridge (vs slightly bulged) and obvious black patches with clear boundaries on the whole body (vs small or moderate dorsal blackish dots in *H. orphicus*).

Hypselotriton huanggangensis sp. nov. differs from *H. orientalis* by its parotoid gland inconspicuous (vs conspicuous) and the presence of obvious black patches with clear boundaries on the dorsum (vs absent in *H. orientalis*).

Hypselotriton huanggangensis sp. nov. differs from *H. glaucus* by its obvious black patches with clear boundaries on the whole body (vs dorsum, flanks, limbs, and upper side of tail with irregular obscure greyish blue patches in *H. glaucus*).

Hypselotriton huanggangensis sp. nov. differs from *H. jiaoren* by its rough skin (vs smooth), and obvious black patches with clear boundaries on the whole body (vs dorsum, flanks, limbs, and upper side of tail uniformly dark brown in *H. jiaoren*).

Hypselotriton huanggangensis sp. nov. differs from *H. maguae* by having its fingers and toes overlapping when forelimbs and hindlimbs are adpressed (vs forelimbs and hindlimbs not meeting when adpressed towards each other along body), and obvious black patches with clear boundaries on the whole body (vs dorsum, flanks, limbs, and upper side of tail uniformly dark brown in *H. maguae*).

Hypselotriton huanggangensis sp. nov. can be distinctly distinguished from *H. wolterstorffi*, *H. cyanurus*, *H. chenggongensis* and *H. yunnanensis* by its absent postocular orange spot (vs present).

Distribution and habitat. *Hypselotriton huanggangensis* sp. nov. is currently known only from the type locality on the western side of the Wuyishan Mountains in northeastern Jiangxi. Newts were found in a small waterhole around mountain shrubs without direct sunlight, at 84 m a.s.l. All individuals were observed in July, September, and February.

Discussion

Despite more than a century of effort, taxonomists have yet to reach a consensus on the concept of species and methods of all species delimitation (Mayden 1997; de Queiroz 1998; Fu and Zeng 2008; Yang and Rannala 2010; Chen et al. 2013; Peng et al. 2014). Trying to solve "the notorious problem of taxonomic uncertainty (Uetz et al. 2024)", Huang et al. (2021) proposed the principle of "species subdivision" with recommendable "subdivision" at the species level. It should help to understand species natural history more effectively and facilitate consistent actions in taxonomy and practices of conservation biology.

In the present study, although the genetic distance based on the ND2 gene fragment between *H. huanggangensis* sp. nov. and its sister species *H. fudingensis* is not very large (uncorrected *p*-distance = 2.2%), morphological differences between them are distinct (Fig. 4; Table 2). In addition, *H. huanggangensis* sp. nov. and *H. fudingensis* are isolated by a series of high mountain ranges, including the Wuyishan and Jiufengshan Mountains. These barriers often isolate different amphibian species (Chen et al. 2020).

With the addition of the new species described here, the genus *Hypselotriton* now includes 11 species. Until now, seven species of *Hypselotriton* were found in the southeastern Chinese hilly area (*H. huanggangensis*, *H. jiaoren*, *H. glaucus*, *H. maguae*, *H. orphicus*, *H. fudingensis* and *H. orientalis*), and another four species of *Hypselotriton* are distributed in southwestern China. Due to unresolved relationships, a more extensive sampling of taxa and molecular data are necessary for reliable conclusions on the evolution and taxonomy of *Hypselotriton*.

Acknowledgements

We thank Cong Liu for assistance in the field. We also thank Ben Liu for discussion of the analysis of phylogenetic data.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This work was supported by the Second Tibetan Plateau Scientific Expedition and Research Program (STEP), Grant No. 2019QZKK0501, Doctoral Research Starting Foundation of Anhui Normal University (752017), National Natural Science Foundation of China (NSFC 31471968; 32001222; 31900323).

Author contributions

Writing–original draft: ZJ. Writing–reviewing and editing: ZJ, SH, JC, JR. Funding acquisition & Supervision: QF, LC, YG. Investigation–sample collection: ZJ, ZC, TZ. Formal analysis–phylogenetic & morphological analysis: ZJ, WL, ZZ, XH.

Author ORCIDs

Zhihao Jiang https://orcid.org/0009-0004-1492-0665
Song Huang https://orcid.org/0000-0001-6786-8523
Qiangyong Fan https://orcid.org/0009-0002-5515-2143
Lin Cheng https://orcid.org/0009-0004-4674-4213
Yanan Gong https://orcid.org/0000-0002-8155-7024
Zhangbo Cui https://orcid.org/0009-0000-1501-0402
Tierui Zhang https://orcid.org/0009-0000-1869-9313
Wenjun Lan https://orcid.org/0009-0005-0690-1082
Zhian Zou https://orcid.org/0009-0001-2556-2590
Xuanzhi Huang https://orcid.org/0009-0008-2873-3640
Jean Raffaëlli https://orcid.org/0000-0003-0567-3661
Jinmin Chen https://orcid.org/0000-0001-6432-7721

Data availability

All of the data that support the findings of this study are available in the main text.

References

AmphibiaChina (2024) The database of Chinese amphibians. http://www.amphibiachina.org/ [Accessed 25 February 2024]

AmphibiaWeb (2024) Information on amphibian biology and conservation. http://amphibiaweb.org/ [Accessed 25 February 2024]

Boulenger GA (1905) Description of a new newt from Yunnan. Proceedings of the Zoological Society of London 1905: 277–278.

Chan LM, Zamudio KR, Wake DB (2001) Relationships of the salamandrid genera *Paramesotriton*, *Pachytriton*, and *Cynops* based on mitochondrial DNA sequences. Copeia 2001(4): 997–1009. https://doi.org/10.1643/0045-8511(2001)001[0997:ROTSGP]2.0.CO;2

Chang MLY (1935) Note préliminaire sur la classification des salamandres d'Asie orientale. Bulletin de la Société Zoologique de France 60: 424–427.

Chen X, Jiang K, Guo P, Huang S, Rao DQ, Ding L, Takeuchi H, Che J, Zhang Y, Myers EA, Burbrink FT (2013) Assessing species boundaries and the phylogenetic position of the rare Szechwan ratsnake, Euprepiophis perlacea (Serpentes: Colubridae), using coalescent–based methods. Molecular Phylogenetics and Evolution 70: 130–136. https://doi.org/10.1016/j.ympev.2013.09.003

Chen ZQ, Tang Y, Wang YY, Li YD, Lin LH, Ding GH (2020) Species Diversity and Elevational Distribution of Amphibians in the Xianxialing and Wuyishan Mountain Ranges, Southeastern China. Asian Herpetological Research 11(1): 44–55. https://doi.org/10.16373/j.cnki.ahr.190038

Chen JM, Suwannapoom C, Wu YH, Poyarkov NA, Xu K, Pawangkhanant P, Che J (2021) Integrative taxonomy reveals a new species of *Leptobrachella* (Anura: Megophryidae) from the mountains of northern Thailand. Zootaxa 5052(2): 41–64. https://doi.org/10.11646/zootaxa.5052.2.2

David A (1873) Quelques renseignements sur l'histoire naturelle de la Chine septentrionale et occidentale. Journal of the North-China Branch of the Royal Asiatic Society. New Series 7: 205–234.

de Queiroz K (1998) The general lineage concept of species, species criteria, and the process of speciation. In: Howard DJ, Berlocher SH (Eds) Endless Forms: Species and Speciation. Oxford University Press, Oxford, UK, 57–75.

Dubois A, Raffaëlli J (2009) A new ergotaxonomy of the family Salamandridae Goldfuss, 1820 (Amphibia, Urodela). Alytes 26(1–4): 1.

Dubois A, Raffaëlli J (2011) Subgeneric taxonomy and nomenclature of the genus *Hypselotriton* Wolterstorff, 1934 (Amphibia, Urodela). Alytes 27(4): 151–153.

Dubois A, Raffaëlli J (2012) A new ergotaxonomy of the order Urodela Duméril, 1805 (Amphibia, Batrachia). Alytes 28(3–4): 77–161.

Dubois A, Ohler A, Pyron RA (2021) New concepts and methods for phylogenetic taxonomy and nomenclature in zoology, exemplified by a new ranked taxonomy of recent amphibians (Lissamphibia). Megataxa 5(1): 1–738. https://doi.org/10.11646/megataxa.5.1.1

Fei L, Ye CY (2016) Amphibians of China (Vol. 1). Beijing, China: Science Press. [In Chinese]

Fei L, Ye CY, Huang YZ (1990) Key to Chinese amphibia. Scientific and Technical Documentation Press. [In Chinese]

Fei L, Hu SQ, Ye CY, Huang YZ (2006) Fauna Sinica. Amphibia. Volume 1 General Accounts of Gymnophiona and Urodela. Beijing, China: Science Press. [In Chinese]

Fei L, Ye CY, Jiang JP (2012) Colored Atlas of Chinese Amphibians and Their Distributions. Sichuan Publishing Group Sichuan Publishing House of Science & Technology. [In Chinese]

Frost DR (2024) Amphibian Species of the World: an Online Reference. Version 6.2. https://amphibiansoftheworld.amnh.org/index.php [Accessed 25 February 2024]

Fu JZ, Zeng XM (2008) How many species are in the genus Batrachuperus? A phylogeographical analysis of the stream salamanders (family Hynobiidae) from southwestern China. Molecular Ecology 17(6): 1469–1488. https://doi.org/10.1111/j.1365-294X.2007.03681.x

Huang RY, Peng LF, Yu L, Huang TQ, Jiang K, Ding L, Chang JK, Yang DC, Xu YH, Huang S (2021) A new species of the genus *Achalinus* from Huangshan, Anhui, China (Squamata: Xenodermidae). Asian Herpetological Research 12(2): 178–187. https://doi.org/10.16373/j.cnki.ahr.200075

Kou Z, Xing Y (1983) A new species of *Cynops* from Yunnan. ActaHerpetologica Sinica. New Series. Chengdu 2(4): 51–54.

Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: Molecular evolutionary genetics analysis across computing platforms. Molecular Biology and Evolution 35(6): 1547–1549. https://doi.org/10.1093/molbev/msy096

Lai JS, Lue KY (2008) Two new *Hynobius* (Caudata: Hynobiidae) salamanders from Taiwan. Herpetologica 64(1): 63–80. https://doi.org/10.1655/06-065.1

Lin P, Ye QH (1985) Vegetation research on Wuyi Mountain Nature Reserve II, Huanggang Mountain Peak Meadow Vegetation. Wuyi Science 1985(5): 255–264. [In Chinese]

Liu CC, Hu SQ, Yang FH (1962) Preliminary report of Amphibia from western Kweichow. Dong Wu Xue Bao 14(3): 381–392.

Lyu ZT, Qi S, Zhang SY, Dai KY, Wang YY (2023) Two New Species of Fire–Bellied Newts (Caudata, Salamandridae, *Cynops*) from Southeastern China. Asian Herpetological Research 14(1): 41–54. https://doi.org/10.16373/j.cnki.ahr.220059

Mayden RL (1997) A hierarchy of species concepts: the denouement in the saga of the species problem. In: Claridge M, Darwah HA, Wilson MR (Eds) Species: the Units of Biodiversity. Chapman & Hall, London, 381–424.

Peng LF, Lu CH, Huang S, Guo P, Zhang YP (2014) A new species of the genus Thermophis (Serpentes: Colubridae) from Shangri-La, northern Yunnan, China, with a proposal for an eclectic rule for species delimitation. Asian Herpetological Research 5(4): 228–239. https://doi.org/10.3724/SP.J.1245.2014.00228

Raffaëlli J (2013) Urodeles du Monde, 2nd edn. Penclen Edition, Plumelec, France, 149–152.

Raffaëlli J (2022) Salamanders & Newts of the World. Penclen Edition, Plumelec, France, 1095 pp.

Rancilhac L, Irisarri I, Angelini C, Arntzen JW, Babik W, Bossuyt F, Künzel S, Lüddecke T, Pasmans F, Sanchez E, Weisrock D, Veith M, Wielstra B, Steinfartz S, Hofreiter M, Philippe H, Vences M (2021) Phylotranscriptomic evidence for pervasive ancient hybridization among Old World salamanders. Molecular Phylogenetics and Evolution 155(106967): 1–14. https://doi.org/10.1016/j.ympev.2020.106967

Risch JP (1983) *Cynops orphicus*, a new salamander from Guangdong Province, South China (Amphibia, Caudata, Salamandridae). Alytes 2: 45–52.

Ronquist F, Teslenko M, Van DMP, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61(3): 539–542. https://doi.org/10.1093/sysbio/sys029

Silvestro D, Michalak I (2012) RaxmlGUI: A graphical front-end for RAxML. Organisms, Diversity & Evolution 12(4): 335–337. https://doi.org/10.1007/s13127-011-0056-0

Tominaga A, Matsui M, Yoshikawa N, Nishikawa K, Hayashi T, Misawa Y, Tanabe S, Ota H (2013) Phylogeny and historical demography of *Cynops pyrrhogaster* (Amphibia: Urodela): taxonomic relationships and distributional changes associated with climatic oscillations. Molecular Phylogenetics and Evolution 66(3): 654–667. https://doi.org/10.1016/j.ympev.2012.10.015

Tschudi, Johann JV (1838) Classification der Batrachier mit Berücksichtigungder fossilen Thiere dieser Abtheilung der Reptilien. Petitpierre, Neuchâtel, Switzerland. https://doi.org/10.5962/bhl.title.4883

Uetz P, Patel M, Gbadamosi Z, Nguyen J, Shoope S (2024) A reference database of reptile images. bioRxiv 2024–03. https://doi.org/10.1101/2024.03.08.584020

Weisrock DW, Papenfuss TJ, Macey JR, Litvinchuk SN, Polymeni R, Ugurtas IH, Zhao E, Jowkar H, Larson A (2006) A molecular assessment of phylogenetic relationships and lineage accumulation rates within the family Salamandridae (Amphibia, Caudata). Molecular Phylogenetics and Evolution 41(2): 368–383. https://doi.org/10.1016/j.ympev.2006.05.008

Wolterstorff W (1934) Über die Gattung Hypselotriton. Zoologischer Anzeiger 108: 257–263.

Wu YK, Wang Y, Jiang K, Hanken J (2010a) A new newt of the genus *Cynops* (Caudata: Salamandridae) from Fujian Province, southeastern China. Zootaxa 2346(1): 42–52. https://doi.org/10.11646/zootaxa.2346.1.4

Wu YK, Wang Y, Jiang K, Hanken J (2010b) Homoplastic evolution of external colouration in Asian stout newts (*Pachytriton*) inferred from molecular phylogeny. Zoologica Scripta 39(1): 9–22. https://doi.org/10.1111/j.1463-6409.2009.00400.x

Yang ZH, Rannala B (2010) Bayesian species delimitation using multilocus sequence data. Proceedings of the National Academy of Sciences of the United States of America 107(20): 9264–9269. https://doi.org/10.1073/pnas.0913022107

Yang DC, Xu YH, Wu JX, Gong YA, Huang RY, Xiang J, Feng ZL, Huang TQ, Huang S (2023) A new species of the genus *Achalinus* (Squamata: Xenodermidae) from Nanning, Guangxi, China. Zootaxa 5319(3): 389–402. https://doi.org/10.11646/zootaxa.5319.3.5

Ye CY, Fei L, Hu SQ (1993) Rare and Economic Amphibians of China. Chengdu, China: Sichuan Publishing House of Science and Technology.

Yuan ZY, Jiang K, Lu SQ, Yang JX, Nguyen QT, Nguyen TT, Jin JQ, Che J (2011) A phylogeny of the *Tylototriton asperrimus* group (Caudata: Salamandridae) based on a mitochondrial study: Suggestions for a taxonomic revision. Zoological Research 32(6): 577–584.

Yuan ZY, Jiang K, Ding LM, Zhang L, Che J (2013) A new newt of the genus *Cynops* (Caudata: Salamandridae) from Guangdong, China. Asian Herpetological Research 4(2): 116–123. https://doi.org/10.3724/SP.J.1245.2013.00116

Yuan ZY, Wu YK, Yan F, Murphy RW, Papenfuss TJ, Wake DB, Zhang YP, Che J (2022) Comparative multi-locus assessment of modern Asian newts (*Cynops*, *Paramesotriton*, and *Pachytriton*: Salamandridae) in southern China suggests a shared biogeographic history. Zoological Research 43(5): 706. https://doi.org/10.24272/j.issn.2095-8137.2022.080

Zhang P, Papenfuss TJ, Wake MH, Qu L, Wake DB (2008) Phylogeny and biogeography of the family Salamandridae (Amphibia: Caudata) inferred from complete mitochondrial genomes. Molecular Phylogenetics and Evolution 49(2): 586–597. https://doi.org/10.1016/j.ympev.2008.08.020

Zhao EM, Hu QX (1984) Studies on Chinese Tailed Amphibians. Sichuan Scientific and Technical Publishing House, Chengdu, China. [In Chinese]

Zhao EM, Hu QX, Jiang YM, Yang YH (1988) Studies on Chinese Salamanders. Oxford, USA: Society for the Study of Amphibians and Reptiles.

Zhong JJ, Zhang ZH, Zheng YM, Zhang YX, Ding GH, Lin ZH (2021) The complete mitochondrial genome of an Asian warty newt, *Paramesotriton aurantius* (Caudata: Salamandridae). Mitochondrial DNA. Part B, Resources 6(2): 428–429. https://doi.org/10.1080/23802359.2020.1870892

ZooKeys 1208: 347–362 (2024)
DOI: 10.3897/zookeys.1208.117056

Research Article

Two new species of *Landouria* Godwin-Austen, 1918 (Gastropoda, Camaenidae) from Thailand, with a key to Thai species

Benchawan Nahok[1], Utain Chanlabut[1], Sakboworn Tumpeesuwan[2], Chanidaporn Tumpeesuwan[2]

1 *Department of General Science, Faculty of Education, Chaiyaphum Rajabhat University, Muang District, Chaiyaphum, 36000, Thailand*
2 *Department of Biology, Faculty of Science, Mahasarakham University, Kantharawichai District, Maha Sarakham, 44150, Thailand*
Corresponding author: Chanidaporn Tumpeesuwan (ctumpeesuwan@yahoo.com)

Abstract

The present work contains descriptions of two new species of *Landouria* and a key to Thai species of this genus. *Landouria bella* **sp. nov.** is described from isolated limestone hills in Ratchaburi and Phetchaburi provinces, western Thailand. This new species is characterized by its small depressed-globose shell without a peripheral keel, the presence of a small, thin lamella on the columellar side of the inner aperture, a long, cylindrical distally bent flagellum, a short penis with a rounded verge, and a short, thick free oviduct and vagina. The second new species, *Landouria monodon* **sp. nov.** is described from sandstone hills in Kalasin Province, northeastern Thailand. This species has a depressed-conic shell with a blunt peripheral keel, a thick prominent lamella on the columellar side of the inner aperture, a short, finger-shaped, distally bent flagellum, and a long penis with a small, short verge.

Key words: Aegistini, Bradybaeninae, radula, reproductive anatomy, shell morphology

Academic editor: Thierry Backeljau
Received: 8 December 2023
Accepted: 8 July 2024
Published: 5 August 2024

ZooBank: https://zoobank.org/ECCF2630-D984-45A8-BF19-DA219F26D495

Citation: Nahok B, Chanlabut U, Tumpeesuwan S, Tumpeesuwan C (2024) Two new species of *Landouria* Godwin-Austen, 1918 (Gastropoda, Camaenidae) from Thailand, with a key to Thai species. ZooKeys 1208: 347–362. https://doi.org/10.3897/zookeys.1208.117056

Introduction

Landouria Godwin-Austen, 1918 is a terrestrial snail genus that is widely distributed in mainland East and Southeast Asia and the Indo-Australian Archipelago (Schileyko 2004; Hirano et al. 2014; Nurinsiyah et al. 2019). The genus is conchologically characterised by having a depressed, usually brownish-corneous shell, with often angular or keeled whorls, a wide umbilicus, and 5–6 moderately convex whorls. The last whorl is usually somewhat deflected and evenly rounded to obtusely angulated at the periphery. The genus is anatomically characterised by the absence of a dart sac and accessory organs, but also by having a short penis, epiphallus, flagellum, and vas deferens; the gametolytic sac is swollen at the base; there is a thin duct at the middle and a globose sac at the distal end (Godwin-Austen 1918).

Seven species of *Landouria* have been previously reported in Thailand as *Aegista* (*Plectotropis*) spp. (Solem 1966; Panha 1996; Hemmen and Hemmen 2001) (see Tumpeesuwan and Tumpeesuwan 2019: table 2). Subsequently, one species has been placed in the genus *Thaitropis* Schileyko, 2004, as *Thaitropis goniochila* (L. Pfeiffer, 1862), based mainly on the presence of the sharp constriction between the epiphallus and the penis. However, Nurinsiyah et al. (2019) synonymized *Thaitropis* with *Landouria*. Nahok et al. (2021) suggested that *Thaitropis* sp. (in Sutcharit et al. 2017: fig. 6–32e) should be classified as *Landouria diplogramma* (Möllendorff, 1902), based on a comparison with voucher specimens deposited in the Naturalis Biodiversity Center (Leiden, the Netherlands), which is labelled as *Plectotropis diplogramme* Möllendorff, 1902 (RMNH.MOL.309867). Preserved specimens from Khao See Siad Ah, Nakhon Ratchasima (NHMSU-00034) (Nahok et al. 2021: figs 3F, 4F) exhibiting shell characters closely correspond with these voucher specimens of *P. diplogramme*. These preserved specimens have a reproductive anatomy that is consistent with typical features of *Landouria*. Therefore, these specimens should be identified as *Landouria diplogramma*.

Boonngam et al. (2008) reported *L. winteriana* (L. Pfeiffer, 1842) and *L. smimensis* (Mousson, 1849) in eastern Thailand. However, both species were previously reported from Sumatra (van Benthem Jutting 1950, 1959; Zilch 1966; von Martens 1867; Schileyko and Kuznetsov 1998; Heryanto 2013; Marwoto 2016; Köhler et al. 2019; Nurinsiyah et al. 2019). Köhler et al. (2019) hypothesized that *L. winteriana* (in Boonngam et al. 2008) may have been confused with an undescribed species, which indicates that there may be additional cryptic species in other localities of *L.* “*winteriana*”. Nurinsiyah et al. (2019) concluded that *L. smimensis* is found only in the Tengger Mountains of East Java, whereas the other records in Central and East Java, Lombok, Bali, and Thailand (Rensch 1931, 1934; Vermeulen and Whitten 1998; Boonngam et al. 2008) most likely represent separate species. Therefore, a comprehensive re-assessment of *L.* “*winteriana*” and *L.* “*smimensis*” in Thailand is required, and it is necessary to re-examine both species as reported by Boonngam et al. (2008).

Recently, six *Landouria* species have been described from northeastern Thailand based on the characters of shell, radula morphology, and reproductive anatomy. These are *L. strobiloides* Tumpeesuwan & Tumpeesuwan, 2019 and five species described by Nahok et al. (2021): *L. circinata*, *L. tuberculata*, *L. trochomorphoides*, *L. chloritoides*, and *L. elegans*.

In this study, we describe two new species, which were discovered on limestone hills in western Thailand and sandstone hills in northeastern Thailand (Fig. 1).

Materials and methods

This study is based on materials collected during surveys by Nahok (2020) in limestone and sandstone hills throughout Thailand from 2018 to 2021. Living snails and empty shells were collected from rocks and leaf litter during the rainy seasons at Khao Bin Cave, Mueang Ratchaburi District, Ratchaburi Province; Khao Nang Panthurat Forest Park, Cha-am District, Phetchaburi Province in western Thailand; and Phu Po, Mueang Kalasin District and Phu Kum Khao, Sahatsakhan District, Kalasin Province in northeastern Thailand (Fig. 1). Most living adult specimens were drowned in water for 24 h and subsequently preserved in 70% ethanol for study of radular morphology and reproductive anatomy. Intact adult shells were used to count the number of whorls and measure shell height (**SH**), shell width (**SW**), aperture height (**AH**), aperture width (**AW**), and umbilicus width (**UW**) using digital vernier calipers. To study the genital

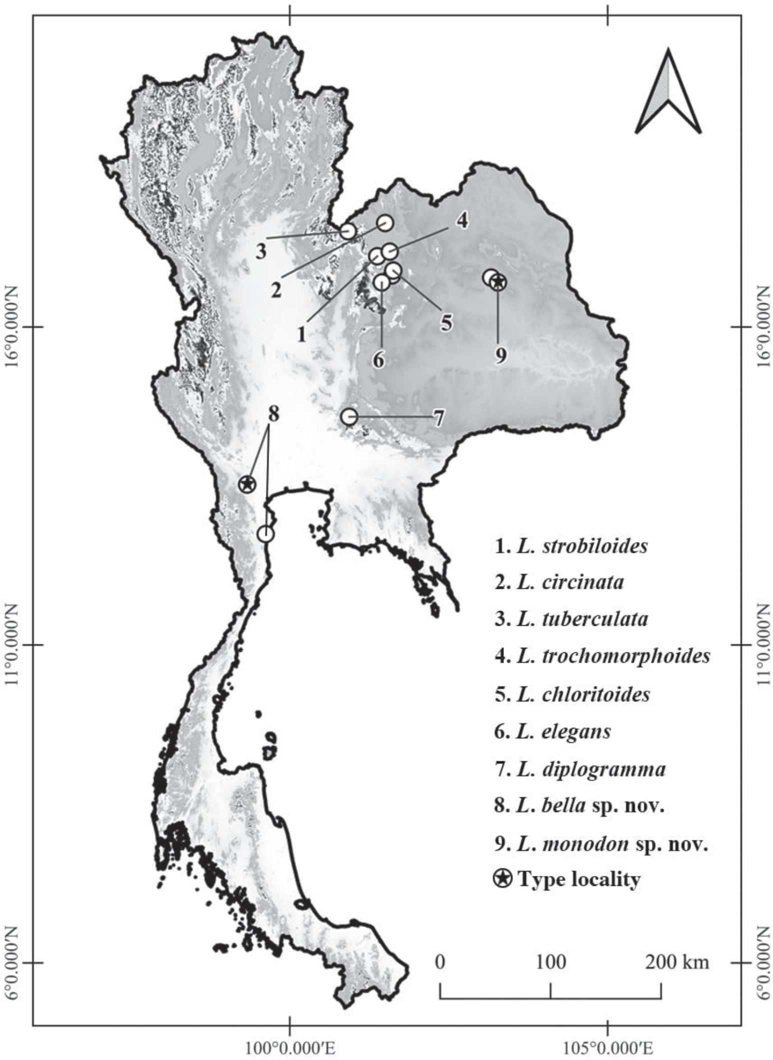


Figure 1. Geographic distribution of verified Thai *Landouria* species and showing the type localities of *L. bella* sp. nov. and *L. monodon* sp. nov.

system and radula, three adult snails from one locality per putative species were dissected under a stereomicroscope. The radulae were extracted from the buccal mass and examined under a scanning electron microscope (SEM), following the methods of Geiger et al. (2007). The material is kept in the following institutions: Natural History Museum, Mahasarakham University (Mahasarakham, Thailand; **NHMSU**); Zoological Research Collection of Muban Chombueng Rajabhat University (Ratchaburi, Thailand; **ZMCRU**); Zoological Research Collection of Chaiyaphum Rajabhat University (Chaiyaphum, Thailand; **ZCPRU**); Muséum National d'Histoire Naturelle (Paris, France; **MNHN**).

The abbreviations used are from Solem (1966) and Pholyotha et al. (2021a, 2021b): **ag**, albumen gland; **at**, atrium; **ep1**, proximal part of epiphallus (from penis side, is the parts before the insertion of the retractor muscle); **ep2**, distal part of epiphallus (is the part from the insertion of the retractor muscle to vas deferens); **fl**, flagellum; **fo**, free oviduct; **gs**, gametolytic sac (= bursa copulatrix); **hd**, hermaphroditic duct; **p**, penis; **prm**, penial retractor muscle; **pro**, prostate gland; **ut**, uterus; **v**, verge; **va**, vagina; **vd**, vas deferens.

Results

Systematics

Family Camaenidae Pilsbry, 1895
Subfamily Bradybaeninae Pilsbry, 1934
Tribe Aegistini Kuroda & Habe, 1949

Genus *Landouria* Godwin-Austen, 1918

Type species. *Helix huttonii* L. Pfeiffer, 1842 (new name for *Helix orbicula* Hutton & Benson, 1838), by original designation.

Type locality. Himalaya near Simla, Mahasu, northern India (Hutton and Benson 1838).

***Landouria bella* Nahok & S. Tumpeesuwan, sp. nov.**
https://zoobank.org/DDCCEAB2-071E-4EB0-83D4-077CF7EE0232
Figs 2–4, Table 1

Landouria sp.16— Nahok 2020: 61; fig. 24G, I, table 3
Landouria sp.—Chanlabut and Nahok 2022: figs 2D, 3D, table 1

Type locality. Thailand, Ratchaburi Province, Mueang Ratchaburi District, Khao Bin Cave, 13°35'37.56"N, 99°39'56.57"E, Isolated limestone hills, alt. 116 m. 7 July 2018. Benchawan Nahok and Utain Chanlabut leg.

Type specimens. *Holotype:* • NHMSU-00056 (Fig. 2A), 1 shell, SH = 8.0 mm, SW = 11.1 mm, AH = 4.3 mm, AW = 4.3 mm, UW = 3.3 mm. ***Paratypes:*** • NHMSU-00057 (Figs 2B, 3, 4) 27 shells, • ZMCRU-0001 11 shells, • ZCPRU-0041 65 shells, • ZCPRU-0042 5 living specimens preserved in ethanol, same leg. and locality as holotype, 27 June 2020. ***Other locality:*** • NHMSU-00058 (Fig. 2C, D) 4 shells, • ZCPRU-0043 7 shells. Thailand, Phetchaburi Province, Cha-am District, Khao Nang Panthurat Forest Park, 12°50'20.27"N, 99°57'6.88"E, Isolated limestone hills, alt. 42 m. 13 Aug. 2017 and 7 July 2018. Benchawan Nahok and Utain Chanlabut leg.

Diagnosis. Shell small, depressed-globose. Body whorl rounded; aperture slightly oval, oblique, with thick, slightly reflected lip. Thin, small lamella present on inner columellar side of aperture. Flagellum large, cylindrical, with bent tip; penis short, small, cylindrical; vagina and free oviduct short, swollen. Basal part of gametolytic sac swollen.

Description. (empty shells = 115, living specimens = 5). ***Shell*** (Fig. 2) dextral, small, depressed-globose; body whorl large, well rounded. Whorls six; suture deep; apex obtuse; spire much elevated. Protoconch smooth; teleoconch with fine, irregular wrinkles, without scaly processes, last whorl with indistinct, incised spiral lines; umbilical side of last whorl with spiral lines more distinct. Umbilicus deep, very wide. Shell dimensions of specimens from type locality (N = 104; mean values in parentheses): shell height 5.7–9.4 mm (6.69 ± 0.71 mm), shell width 8.5–12.2 mm (10.54 ± 0.65 mm), aperture height 3.2–5.3 mm (4.47 ± 0.38 mm), aperture width 2.9–5.1 mm (4.08 ± 0.34 mm), and umbilicus width 2.7–5.4 mm (3.60 ± 0.33 mm). Shell dimensions of specimens from Khao Nang Panthurat (N = 11): shell height 5.81–7.09 mm (6.45 ± 0.64 mm), shell width

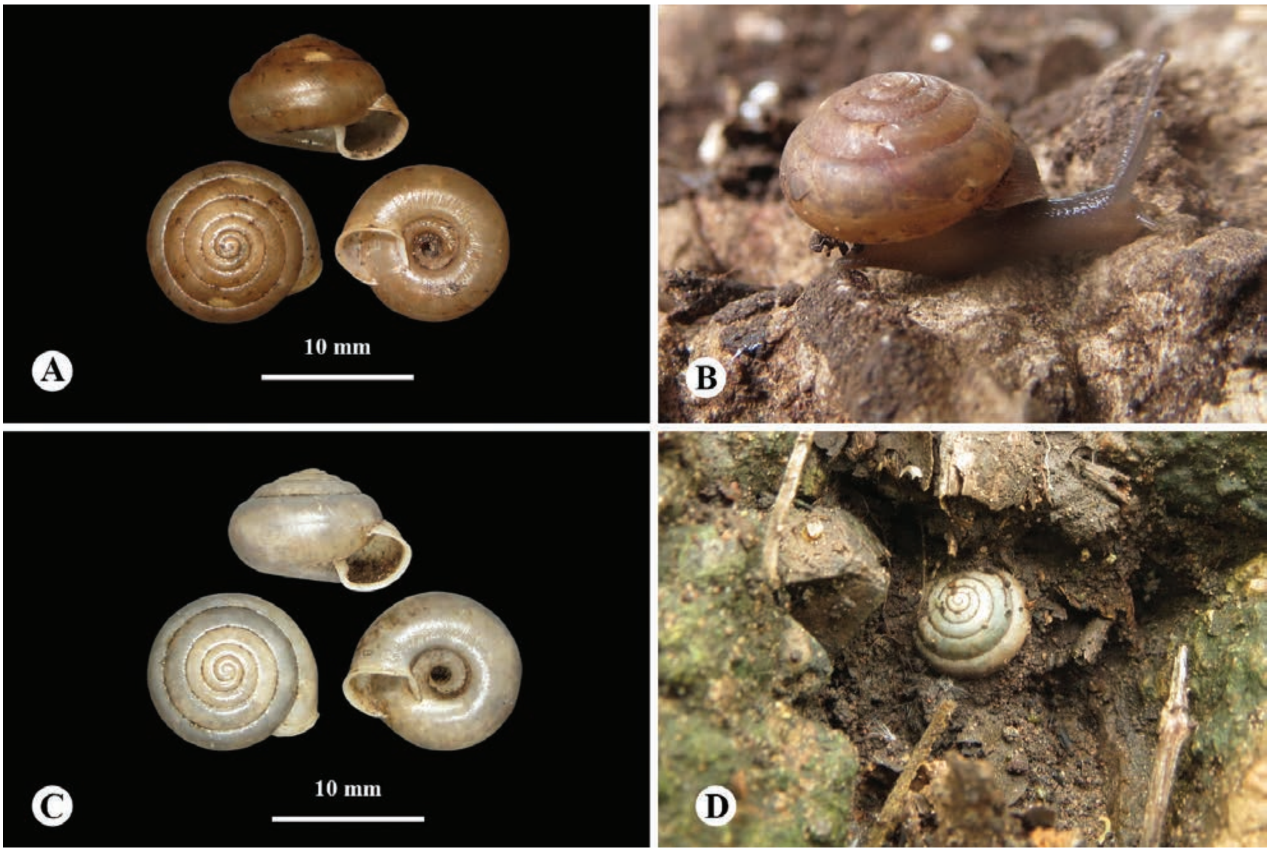


Figure 2. *Landouria bella* sp. nov. **A** holotype (NHMSU-00056) **B** paratype (ZCPRU-0042) **C, D** empty shell from Khao Nang Panthurat Forest Park, Phetchaburi Province (NHMSU-00058).

9.59–10.87 mm (10.23 ± 0.64 mm), aperture height 4.13–4.73 mm (4.43 ± 0.30 mm), aperture width 3.64–4.38 mm (4.01 ± 0.37 mm), and umbilicus width 3.25–3.83 mm (3.54 ± 0.29 mm).

Genital system (*N* = 3) (Fig. 3). Atrium short. Penis small, cylindrical, shorter than flagellum, internally with four smooth, longitudinal pilasters, which gradually become corrugated at distal part close to verge. Verge short, swollen (Fig. 3B). Penial retractor muscle present. Proximal part of epiphallus (ep1) approximately equal to length of penis and vagina combined, but thicker and larger than penis. Distal part of epiphallus (ep2) extremely short. Flagellum apically joins epiphallus, more than twice as long as penis, regularly long-cylindrical, bent at distal end, internally with three smooth, longitudinal pilasters (Fig. 3C). Vas deferens a thin, cylindrical tube, laterally entering epiphallus. Vagina short, distally globularly dilated, internally with five thick, longitudinal pilasters (Fig. 3D). Free oviduct shorter than vagina. Proximal part of gametolytic sac very stout, swollen, with a long, narrow, cylindrical tube, and with at its distal end sac-like, small, swollen, and spherical. Prostate gland very long; uterus long, swollen.

Radula (*N* = 3) Comprises 103–107 transverse rows with 63–71 teeth per row; radular formula: (22–24)+(6–8)+1+(6–8)+(22–24). Central tooth usually symmetric, unicuspid, lanceolate (Fig. 4B). Lateral teeth quite like central tooth, but oblique, larger, and longer. Teeth on both sides begin to transform into indistinct bicuspid marginal teeth with tiny ectocone at tooth number 6–8 (Fig. 4C) and gradually change from bicuspid to tricuspid; endocone small; mesocone large, lanceolate; ectocone triangular, with 2–4 tiny cusps (Fig. 4D).

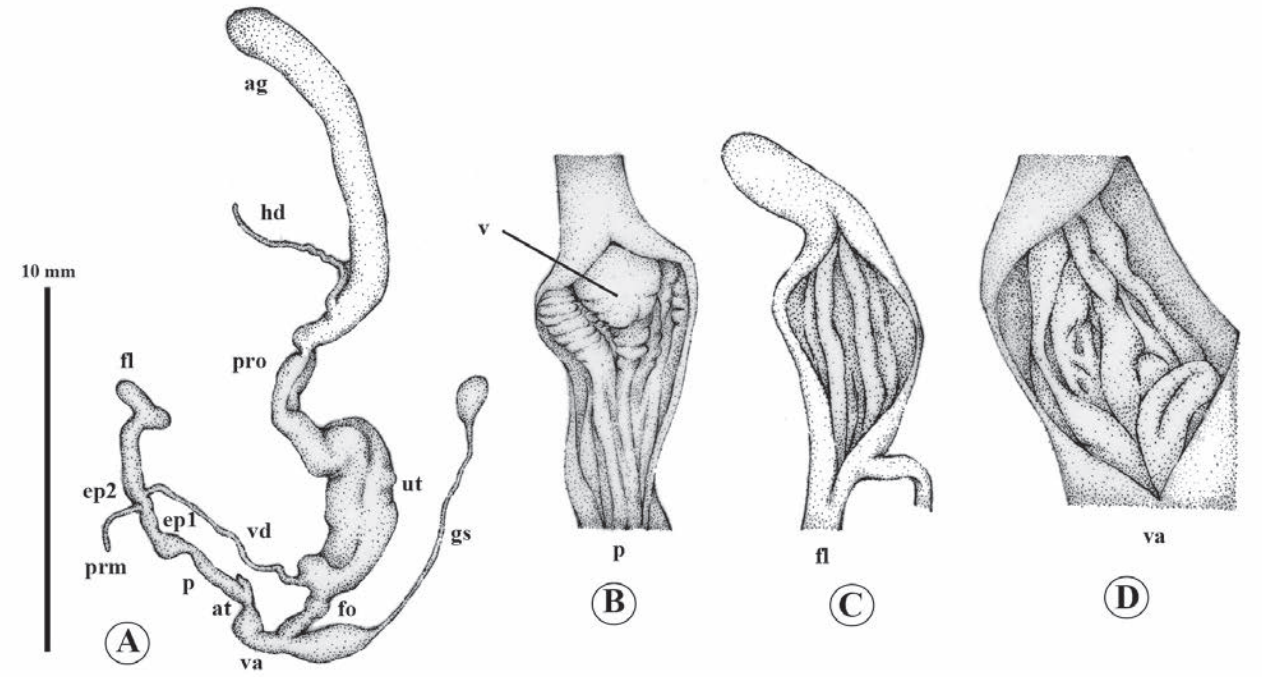


Figure 3. Genital anatomy of *Landouria bella* sp. nov., paratype (ZCPRU-0042) **A** whole genitalia **B–D** internal wall sculpture of **B** penis (p) **C** flagellum (fl) **D** vagina (va).

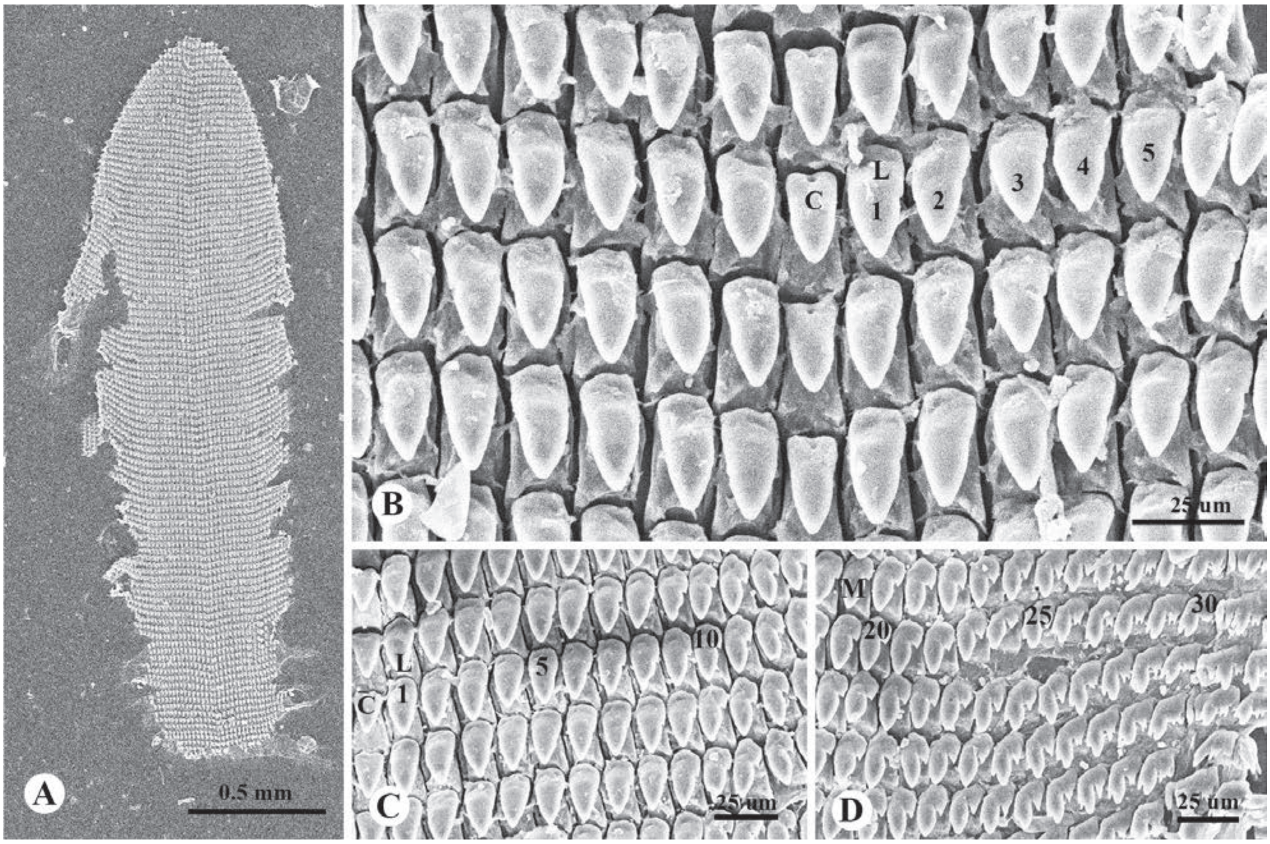


Figure 4. Radula morphology of *Landouria bella* sp. nov., paratype (ZCPRU-0042) **A** whole radula **B** close-up view of central tooth and lateral teeth **C** right side of central tooth and lateral teeth **D** right side of marginal teeth. Numbers indicate order of lateral and marginal teeth. Abbreviation: C = central tooth, L = lateral teeth, M = marginal teeth.

Table 1. Comparison of shells, genital systems and radulae of Thai *Landouria* species. Reference: 1 = Tumpeesuwan and Tumpeesuwan (2019); 2 = Nahok et al. (2021); 3 = this study; 4 = Schileyko (2011) (question mark = no data).

Characters	***L. strobiloides***	***L. circinata***	***L. tuberculata***	***L. trochomorphoides***	***L. chloritoides***	***L. elegans***	***L. diplogramma***	***L. bella* sp. nov.**	***L. monodon* sp. nov.**	***L. ptychostyla***
Shell:										
Shell shape	Conical-lenticular	Conical-lenticular	Slightly convex	Subconvex	Depressed	Conical	Sub-globose	Globose	Depressed-conical	Depressed-conical
Number of whorls	5 ½	6	6 ½	6	6 ½	6	5 ½	6	5 ¾	6
Peripheral band	Dark brown	Pale brown	Absent	Brown	Absent	Dark brown	Pale brown	Absent	Absent	Absent
Periphery keel	Sharp	Sharp	Moderate	Sharp	Weak	Sharp	Very weak	Absent	Slightly	Moderate
Scale sculpture	Absent	Absent	Tubercle	Scaly	Absent	Absent	Absent	Absent	Absent	Absent
Lamella at inner aperture	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Present (thin)	Present (sharp)	Present (thin)
Genital system:										
Penis	Short, slightly stout	Long cylindrical	Swollen	Long slender	Very large and stout	Long cylindrical	Swollen	Small cylindrical	Long cylindrical	Long fusiform
Verge	?	Present	Present	Absent	Present	Absent	Present	Present	Present	Absent
Flagellum	Strobilus-shaped	Circinate-shaped	Protrusion	Slender towards tip	Narrow ovate	Water drop-shaped	Short protrusion	Cylindrical, bent tip	Cylindrical, bent tip	Shot, hook-shape
Basal part of gametolytic sac	Swollen	Thick and stout	Thin	Thin	Thick	Stout	Thick	Swollen	Swollen	Swollen
Radula:										
Number of rows	100	93–95	126–130	107–111	125–129	110–114	121–125	103–107	136–140	?
Number of teeth in each row	3–53	55–63	79–87	65–73	75–83	69–77	61–69	63–71	63–71	?
- Lateral teeth	8–10	8–10	11–13	8–10	11–13	12–14	7–9	6–8	12–14	?
- Marginal teeth	15–17	19–21	28–30	24–26	26–28	22–24	23–25	22–24	19–21	?
Central tooth	Elongate-lanceolate	Tongue-shaped	Slender-lanceolate	Short-lanceolate	Lanceolate	Tongue-shaped	Triangular	Lanceolat	Triangular	?
References	1	2	2	2	2	2	2	3	3	4

Etymology. Specific epithet "*bella*" is derived from the Latin word "bellus", which means lovely fine, pretty, and beauty. This name refers to the lovely shell of the new species.

Habitat. This species inhabits isolated limestone hills, where it lives on rocks and the ground in a natural forest at the foot of limestone cliffs.

Distribution. *Landouria bella* sp. nov. is currently known only from Khao Bin Cave, Ratchaburi Province, and Khao Nang Panthurat Forest Park, Phetchaburi Province, in western Thailand (Fig. 1).

Remarks. The new species is distinguished from other species of *Landouria* in Thailand by its depressed-globose shell, the presence of a thin, small columellar lamella on the inner side of the aperture, and the absence of an angular and peripheral keel (Fig. 2). Its genital system is distinguished by its flagellum, which is regularly cylindrical, with a bent tip. The internal structure of the penis has a rounded swollen verge and resembles that of *L. circinata*, as well as *L. tuberculata* from Loei, *L. chloritoides* from Khon Kaen, and *L. diplogramma* from Nakhon Ratchasima, northeastern Thailand, but the new species differs in having the proximal part of the penis with thin longitudinal pilasters and the distal part which becomes gradually corrugated (Fig. 3B). Most radular characteristics are quite similar to those of other species, except for the central tooth, which is lanceolate (Fig. 4B).

Landouria monodon **Nahok & C. Tumpeesuwan, sp. nov.**

https://zoobank.org/11969825-6F9C-4FD2-BB73-5936301502E8
Figs 5D–E, 6, 7, Tables 1, 2

Landouria sp. 1—Ounchareon 2016: 27–32, fig. 4.1A, B, table 4.3
Landouria sp. 2—Nahok 2020: 43–44, fig. 23B, C, table 3

Type locality. Thailand, Kalasin Province, Mueang Kalasin District, Phu Po, 16°37'10.42"N, 103°37'55.59"E, Sandstone hills, alt. 241 m. 17 Jun. 2017. Benchawan Nahok and Utain Chanlabut leg.

Type material. ***Holotype:*** • NHMSU-00059 (Fig. 5D). 1 shell, SH = 6.4 mm, SW = 10.3 mm, AH = 3.4 mm, AW = 4.0 mm, UW = 2.9 mm. ***Paratypes:*** • NHMSU-00060, (Figs 6, 7) 12 shells, • ZCPRU-0045 7 shells, • NHMSU-000613 living specimens preserved in ethanol, • ZCPRU-0046 2 living specimens preserved in ethanol, same leg. and locality as holotype, 26 Sep. 2017.

Other material. • NHMSU-00062 (Fig. 5E) 4 shells, • ZCPRU-0047 4 shells. Thailand, Kalasin Province, Sahatsakhan District, Phu Kum Khao, 16°41'41.98"N, 103°31'34.43"E, Sandstone hills, alt. 267 m, 17 June 2017. Benchawan Nahok and Utain Chanlabut leg.

Diagnosis. Shell small, depressed-conical, slightly keeled; aperture oval, oblique, with thick, reflected lip. Thick prominent lamella present on inner columellar side of aperture. Flagellum short, bend at apical portion. Penis long, large, cylindrical. Free oviduct short; vagina long, distally swollen. Basal part of gametolytic sac enlarged, swollen.

Description. (empty shells = 28, living specimens = 5). ***Shell*** (Fig. 5D, E) dextral, small, depressed-conical. Whorls 5¾–6¼; apex obtuse. Body whorl slightly keeled. Protoconch almost smooth; teleoconch with irregular wrinkles, indistinct incised spiral lines, without scaly processes. Prominent but tiny lamella present on inner columellar side of aperture. Umbilicus deep, wide. Shell dimensions of specimens from type locality (N = 20; mean values in parentheses): shell height 3.10–6.60 mm (4.68 ± 1.04 mm), shell width 5.10–10.40 mm (7.67 ± 1.24 mm), aperture height 2.10–3.50 mm (2.64 ± 0.39 mm), aperture width 2.20–4.10 mm (3.26 ± 0.55 mm), and umbilicus width 2.20–3.00 mm (2.49 ± 0.20 mm). Shell dimensions of specimens from Phu Kum Khao (N = 8): shell height 3.64–4.68 mm (4.85 ± 0.88 mm), shell width 6.43–7.67 mm (7.75 ± 1.33 mm), aperture height 2.25–2.64 mm (2.80 ± 0.35 mm), aperture width 2.71–3.26 mm (3.15 ± 0.48 mm), and umbilicus width 2.29–2.49 mm (2.60 ± 0.20 mm).

Genital system (N = 3) (Fig. 6). Atrium short. Penis cylindrical, longer than flagellum, internally with four corrugated, longitudinal pilasters, distally giving rise to densely interlocked longitudinal rows to verge. Verge small, short (Fig. 6B).

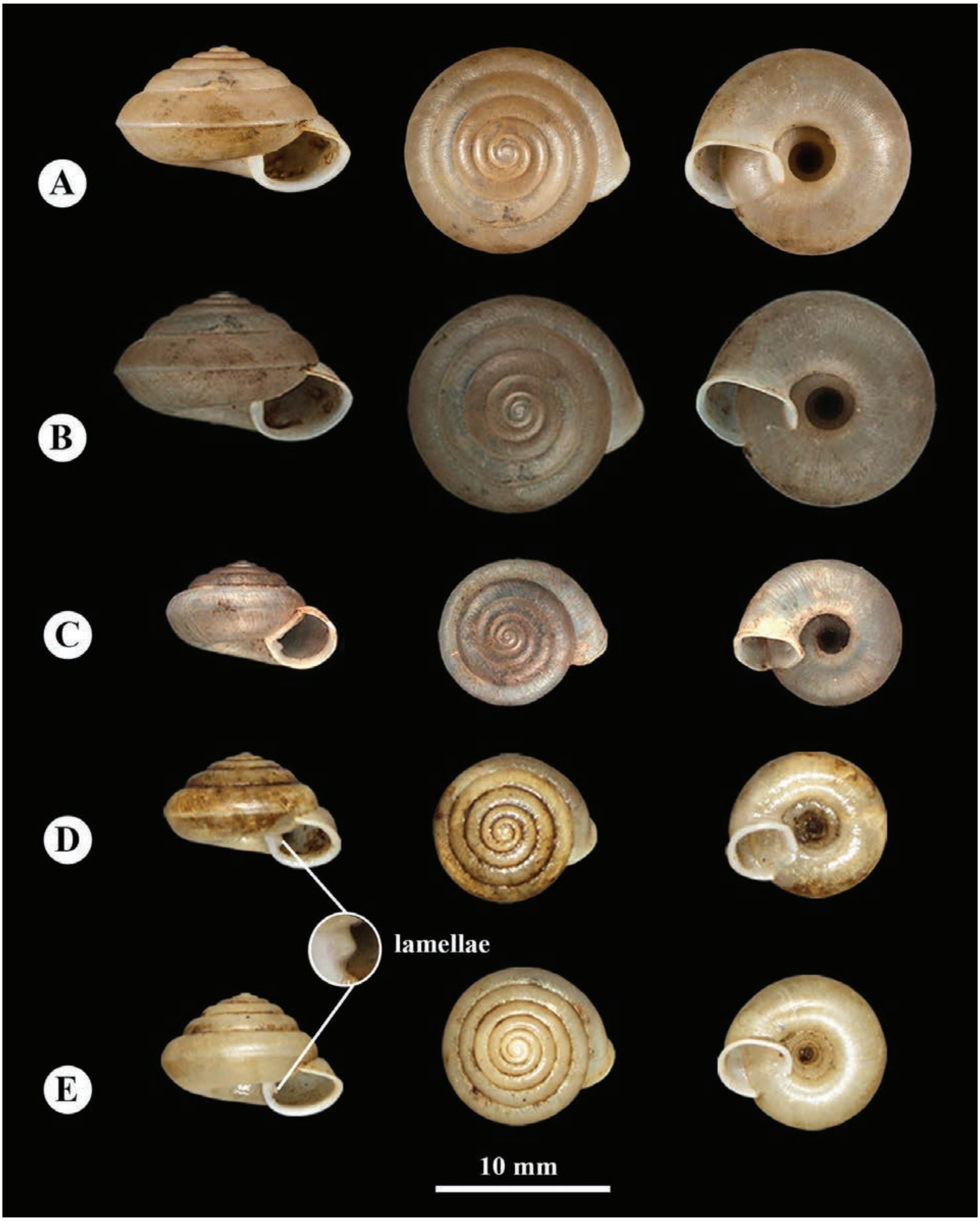


Figure 5. A, B *Helix goniochila* L. Pfeiffer, 1862 syntype (MNHN-2000-1901) **C** *Helix ptychostyla* L. Pfeiffer, 1862 syntype (MNHN-2000-1974) **D, E** *Landouria monodon* sp. nov. **D** holotype (NHMSU-00059) **E** empty shell from Phu Kum Khao, Kalasin Province (NHMSU-00062). Photographs by: **A** Manuel Caballer (MNHN) E-Recolnat Project (ANR-11-INBS-0004); **C** Brabant D (MNHN); **D–E** Benchawan Nahok.

Penial retractor muscle present. Proximal part of epiphallus (ep1) shorter than half of penis length. Distal part of epiphallus (ep2) very short. Flagellum approximately as long as proximal part of epiphallus, regularly short-cylindrical, slight-

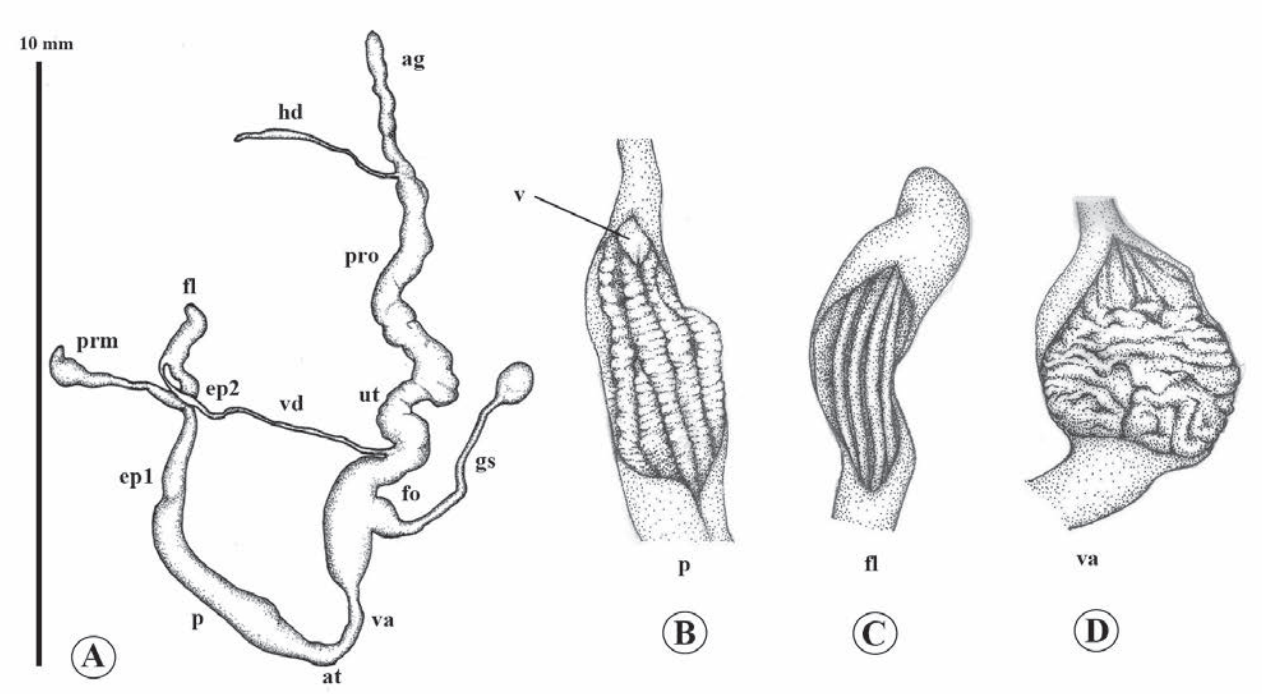


Figure 6. Genital anatomy of *Landouria monodon* sp. nov., paratype (NHMSU-00061) **A** whole genitalia **B–D** internal wall sculpture of **B**, penis (p) **C** flagellum (fl) **D** vagina (va).

ly bent at the tip, internally with four smooth, longitudinal pilasters (Fig. 6C). Vas deferens a thin cylindrical tube, apically entering epiphallus. Vagina long, distally swollen, internally with thick, undulating, transverse pilasters (Fig. 6D). Free oviduct shorter than vagina. Gametolytic sac swollen at base, short cylindrical tube, and with swollen spherical sac at distal end. Prostate gland long; uterus swollen.

Radula (*N* = 3). Comprises 136–140 transverse rows with 63–71 teeth per row (Fig. 7B); radular formula: (19–21)+(12–14)+1+(12–14)+(19–21). Central tooth usually symmetric, small, tricuspid, triangular. Lateral teeth short, bicuspid, with tiny ectocone and gradually changing into tricuspid marginal teeth; endocone small; mesocone large, long, with curved margins; ectocone triangular, with 2–4 tiny cusps (Fig. 7C).

Etymology. Specific epithet "*monodon*" is derived from the Greek words, "monos", one or single, and "odous", tooth, and refers to the single prominent lamella on the inner columellar side of aperture.

Habitat. This new species lives on sandstone hills under leaf litter, in rock crevices, hollow trees, etc. at bases of hills in dry, dipterocarp forest.

Distribution. *Landouria monodon* sp. nov. is currently known from separate sandstone hills, at Phu Po and Phu Kum Khao, Kalasin Province, northeastern, Thailand (Fig. 1).

Remarks. *Landouria monodon* sp. nov. differs from other Thai species of *Landouria* by its tiny but prominent columellar lamella on the inner side of the aperture (Fig. 5D, E). Its genital system and radula are quite similar to *L. diplogramma* from Nakhon Ratchasima, northeastern Thailand, but the new species differs in having its penis not divided into two short portions and its vagina thicker (Fig. 6). The radular central tooth is triangular but differs by its smaller size (Fig. 7). Conchologically, *L. monodon* sp. nov. closely resembles *Helix ptychostyla* L. Pfeiffer,

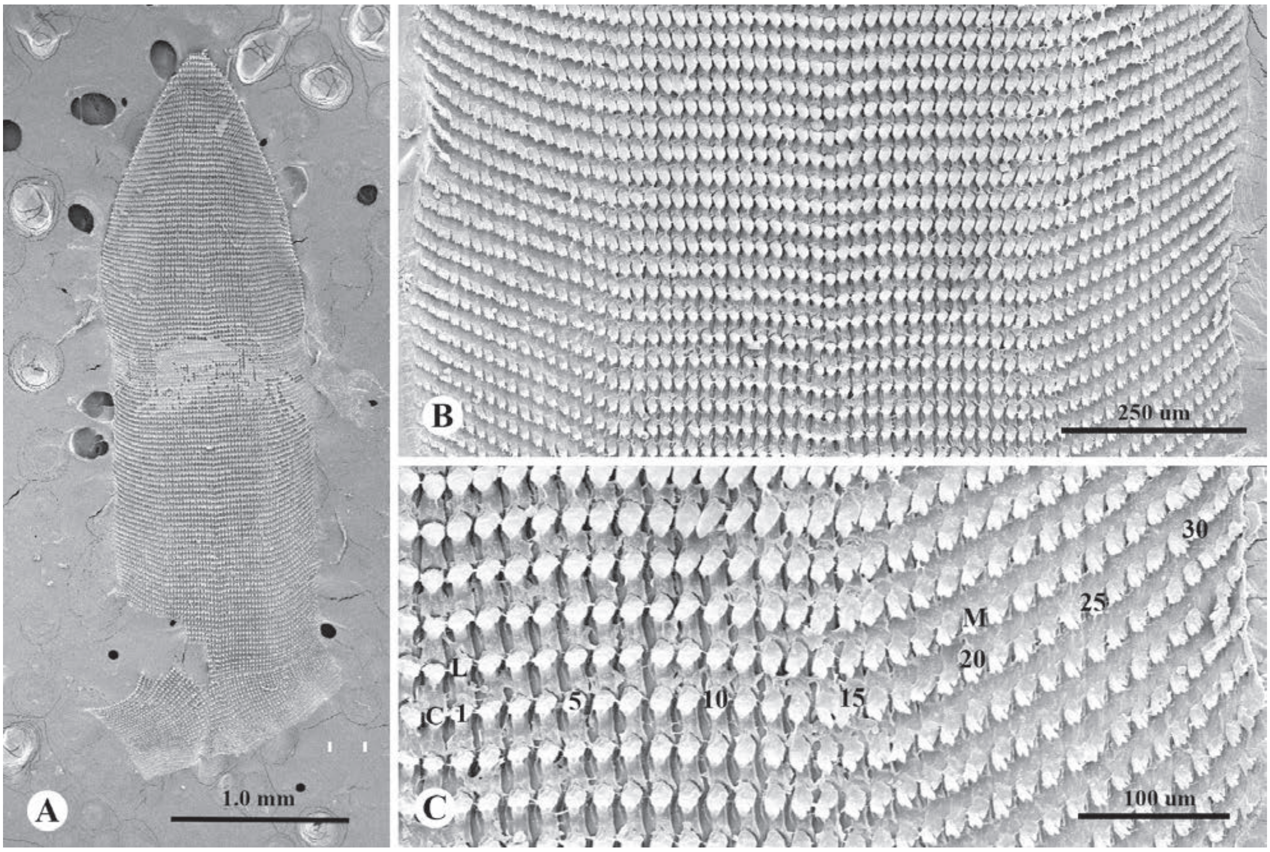


Figure 7. Radula morphology of *Landouria monodon* sp. nov., paratype (NHMSU-00061) **A** whole radula **B** view of transverse rows of radula **C** right side of central tooth, lateral teeth, and marginal teeth. Numbers indicate order of lateral and marginal teeth. Abbreviation: C = central tooth, L = lateral teeth, M = marginal teeth.

Table 2. History of Scientific name changes of *Landouria ptychostyla* (von Martens, 1860) and *L. ptychostyloides* (Schileyko, 2011).

Authors	*L. ptychostyla* (von Martens, 1860)	*L. ptychostyloides* (Schileyko, 2011)
von Martens (1860)	*Helix ptychostyla* von Martens, 1860	–
Pfeiffer (1862)	*Helix goniochila* Pfeiffer, 1862	*Helix ptychostyla* Pfeiffer, 1862
Panha (1996)	*Aegista goniochila* (L. Pfeiffer, 1862)	–
Schileyko (2004)	*Thaitropis goniochila* (L. Pfeiffer, 1862)	–
Schileyko (2011)	*Thaitropis ptychostyla* (von Martens, 1860)	*Thaitropis ptychostyloides*, Schileyko, 2011
Nurinsiyah et al. (2019)	*Landouria ptychostyla* (von Martens, 1860)	*Landouria ptychostyloides* (Schileyko, 2011)

1862, whose types specimen are in MNHN (MNHN-IM-2000-1974; Fig. 5C). (https://www.gbif.org/occurrence/1019688902). Still, the two species differ by many characters: (1) parietal callus prominent in *H. ptychostyla*, but faint or absent in *L. monodon* sp. nov.; (2) last whorl and lip descending in front in *L. monodon* sp. nov.; (3) growth lines prominent in *H. ptychostyla*, but faint in *L. monodon* sp. nov.; (4) umbilical keel absent in *H. ptychostyla*, but prominent in *L. monodon* sp. nov.

Moreover, the type material of *H. ptychostyla* L. Pfeiffer, 1862 likely comes from the Henri Mouhot expedition to Thailand and Laos, which included Bangkok, Wat Phra Phutthachai Saraburi, Korat, Chaiapume, Leute, Kenne Tao, Paklaie, and Thadua (see Inkhavilay et al. 2019: fig. 1), which is over 150 km away from the type locality of *L. monodon* sp. nov.

Recently, Schileyko (2011) proposed that *Helix ptychostyla* was preoccupied by von Martens (1860) and indicated that *H. goniochila* L. Pfeiffer, 1862 (Figs 5A, B) is a synonym of *H. ptychostyla* von Martens, 1860. He used *Thaitropis ptychostyla* (von Martens, 1860) as the available name for this taxon, whereas *T. ptychostyloides* was proposed as *nomen novum* for *Helix ptychostyla* L. Pfeiffer, 1862 (Table 2).

Discussion

A unique characteristic shared by all members of *Landouria* in Thailand is the absence of a dart sac and stimulatory organs, a character combination that is thought to define the family Camaenidae (Páll-Gergely et al. 2013). We agree with Köhler et al. (2019), Nurinsiyah et al. (2019), Tumpeesuwan and Tumpeesuwan (2019), and Páll-Gergely et al. (2020) in rejecting the proposal by Hirano et al. (2014) to treat *Landouria* as a junior synonym of *Aegista*, on account that *Aegista* possesses both a dart sac and stimulatory organs and its geographic distribution is disjunct from *Landouria*. *Landouria* and *Aegista* are two well-differentiated genera, with *Landouria* being distinguished by, for example, its small, depressed shell; broad, open umbilicus; and the presence of a flagellum of various shapes.

Landouria bella sp. nov. differs from all other recently verified Thai *Landouria* species by its depressed-globose shell. Other Thai *Landouria* species usually have a slight to pronounced angular keel at the periphery, as seen in *L. monodon* sp. nov. The existence of a small, thin columellar lamella on the inner side of the aperture of *L. bella* sp. nov. (Fig. 2A, C) resembles *L. monodon* sp. nov. (Fig. 5D, E), but this columellar lamella is prominent in the latter species.

We present below an updated and improved dichotomous identification key to the *Landouria* species of northeastern Thailand based on Nahok et al. (2021).

Key to Thai *Landouria* species by shell morphology

1	Shell without peripheral keel	**2**
–	Shell with peripheral keel	**3**
2	Shell depressed-globose, without brown band	***L. bella* sp. nov.**
–	Shell low-conical, with brown band	***L. diplogramma***
3	Inner side of aperture with prominent columellar lamella	***L. monodon* sp. nov.**
–	Inner side of aperture without columellar lamella	**4**
4	Peripheral keel blunt	***L. chloritoides***
–	Peripheral keel sharp	**5**
5	Peripheral keel slightly sharp, shell surface with numerous tiny tubercles	***L. tuberculata***
–	Peripheral keel very sharp, shell surface without tubercles	**6**
6	Shell with low spire, shell surface with radial scaly processes	***L. trochomorphoides***
–	Shell with high spire, shell surface without radial scaly processes	**7**
7	Keel with downward bent rim	***L. elegans***
–	Keel without downward bent rim	**8**
8	Suture indented, growth line obvious	***L. strobiloides***
–	Suture not indented, growth line obscure	***L. circinata***

Key to Thai *Landouria* species by genital characters

1 Penis shorter than vagina; flagellum strobilus-like .... ***L. strobiloides***

– Penis longer than vagina; flagellum non-strobilus-like **2**

2 Flagellum circinate .... ***L. circinata***

– Flagellum a short protrusion: ovate, slender, or long cylindrical **3**

3 Inner sculpture of penis with parallel, transverse folds .... ***L. trochomorphoides***

– Inner sculpture of penis with longitudinal pilasters **4**

4 Rounded verge absent .... ***L. elegans***

– Rounded verge present **5**

5 Epihallus clearly divided into two portions (ep1 and ep2) .... ***L. diplogramma***

– Epihallus not clearly divided into two portions (ep2 is very short) **6**

6 Vagina as long as free oviduct .... ***L. chloritoides***

– Vagina length not as long as free oviduct **7**

7 Basal part of gametolytic sac slightly swollen .... ***L. tuberculata***

– Basal part of gametolytic sac swollen **8**

8 Inner sculpture of vagina thick longitudinal folds pilasters .... ***L. bella* sp. nov.**

– Inner sculpture of vagina thick undulating transverse pilasters .... ***L. monodon* sp. nov.**

Acknowledgements

We are grateful to the Hin Kong Sub-district Administration Organization for allowing us to conduct research in Khao Bin. We would like to thank the teams from Mahasarakham University for their assistance in sample collection. We wish to express our sincere gratitude to Nual-anong Wichaikul and the staff of the Centre for Scientific and Technological Equipment at Suranaree University of Technology for their valuable support in sample processing and SEM work. We thank Adrian Roderick Plant, a native English speaker, who helped check the language in the manuscript. We deeply thank Thierry Backeljau and the three reviewers, Barna Páll-Gergely, Frank Köhler, and Junn Kitt Foon for their advice and comments. Special thanks are given to Virginie Héros, who kindly advised us on the use of photographs from the MNHN website. This research was performed in accordance with the Animal Care and Use Protocol Review No. IACUC-U1-06867-2560.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This research was financially supported by a Thailand Science Research and Innovation (TSRI) grant to the corresponding author.

Author contributions

Conceptualization: BN, ST, CT. Data curation: BN, ST, CT, UC. Formal analysis: BN, ST. Funding acquisition: ST, CT. Investigation: BN, ST, CT, UC. Methodology: BN, CT, UC. Project administration: BN, CT. Resources: BN, UT. Validation: BN, ST, CT. Visualization: BN, UC. Writing-original draft: BN, UC. Writing-review and editing: CT, ST.

Author ORCIDs

Benchawan Nahok https://orcid.org/0009-0009-1788-6788
Utain Chanlabut https://orcid.org/0000-0001-8275-7434
Sakboworn Tumpeesuwan https://orcid.org/0000-0001-5900-7862
Chanidaporn Tumpeesuwan https://orcid.org/0000-0003-2066-1271

Data availability

All of the data that support the findings of this study are available in the main text.

References

Boonngam P, Dumrongrojwattana P, Matchacheep S (2008) The diversity of land snail fauna in Chonburi Province, Eastern Thailand. Witthayasan Kasetsat Witthayasat 42: 256–263.

Chanlabut U, Nahok B (2022) Species diversity and abundance of land snails in Khao Bin limestone hills, Ratchaburi Province. Life Sciences and Environment Journal 23(1): 259–270. https://doi.org/10.14456/lsej.2022.20

Geiger DL, Marshall BA, Ponder WF, Sasaki T, Warén A (2007) Techniques for collecting, handling, preparing, storing and examining small molluscan specimens. Molluscan Research 27(1): 1–50. https://doi.org/10.11646/mr.27.1.1

Godwin-Austen HH (1918) Zoological results of the Abor Expedition, 1911–12. 49, Mollusca, 9. Records of the Indian Museum 8: 601–621. https://doi.org/10.26515/rzsi/v8/i12/1918/163139

Hemmen J, Hemmen C (2001) Aktualisierte Liste der terrestrischen Gastropoden Thailands. Schriften zur Malakozoologie aus dem Haus der Nature—Cismar 18: 35–70.

Heryanto (2013) Keanekaragaman dan kepadatan Gastropoda terestrial di perkebunan Bogorejo kecamatan Gedongtataan kabupaten Pesawaran provinsi Lampung. Zoo Indonesia 22: 23–29.

Hirano T, Kameda Y, Kimura K, Chiba S (2014) Substantial incongruence among the morphology, taxonomy, and molecular phylogeny of the land snails *Aegista*, *Landouria*, *Trishoplita*, and *Pseudobuliminus* (Pulmonata: Bradybaenidae) occurring in East Asia. Molecular Phylogenetics and Evolution 70: 171–181. https://doi.org/10.1016/j.ympev.2013.09.020

Hutton T, Benson WH (1838) On the land and fresh-water shells of the western Himalaya. Journal of the Asiatic Society of Bengal 7: 211–218.

Inkhavilay K, Sutcharit C, Bantaowong U, Chanabun R, Siriwut W, Srisonchai R, Pholyotha A, Jirapatrasilp P, Panha S (2019) Annotated checklist of the terrestrial molluscs from Laos (Mollusca, Gastropoda). ZooKeys 834: 1–166. https://doi.org/10.3897/zookeys.834.28800

Köhler F, Shea M, Kessner V (2019) Two new species of *Landouria* Godwin Austen, 1918 from Timor-Leste (Stylommatophora, Camaenidae). Molluscan Research 39(3): 253–264. https://doi.org/10.1080/13235818.2018.1557780

Kuroda T, Habe T (1949) Helicacea. Sanmeisha, Tokyo, 6 + 129 pp. [1 pl.] [in Japanese]

Marwoto RM (2016) The occurrence of the terrestrial snail from Sumatra (Mollusca, Gastropoda). Zoo Indonesia 25: 8–21.

Möllendorff OF (1902) Neue Arten und Unterarten von Fruhstorfer in Siam gesammelt. Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft 34: 153–160.

Mousson A (1849) Die Land- und Süsswasser-Mollusken von Java. Nach den Sendungen des Herrn Seminardirektors Zollinger zusammengestellt und beschrieben. F. Schulthess, Zürich, 126 pp. [22 pl.] https://doi.org/10.5962/bhl.title.14346

Nahok B (2020) Systematics and Taxonomy of Land Snails Genera *Aegista*, *Thaitropis*, *Landouria*, and *Pseudobuliminus* in Thailand. Unpublished PhD Thesis, Department of Biology, Faculty of Science, Mahasarakham University, Maha Sarakham.

Nahok B, Tumpeesuwan S, Tumpeesuwan C (2021) Five new species of the land snail genus *Landouria* Godwin-Austen, 1918 (Gastropoda, Camaenidae) from northeastern Thailand, with note on genitalia and radula morphology of *Landouria diplogramma* (Möllendorff, 1902). European Journal of Taxonomy 767: 142–166. https://doi.org/10.5852/ejt.2021.767.1495

Nurinsiyah AS, Neiber MT, Hausdorf B (2019) Revision of the land snail genus *Landouria* Godwin-Austen, 1918 (Gastropoda, Camaenidae) from Java. European Journal of Taxonomy 526(526): 1–73. https://doi.org/10.5852/ejt.2019.526

Ounchareon J (2016) Taxonomy of Land Snail Genus *Landouria* Godwin-Austen, 1918 in Northeastern Thailand. Unpublished Master’s Thesis. Department Faculty of Science, Mahasakham University, Maha Sarakham, 123 pp. [In Thai with English Abstract]

Páll-Gergely B, Hunyadi A, Asami T (2013) A peculiar new species in the genus *Landouria* Godwin-Austen, 1918 from China (Gastropoda: Heterobranchia: Stylommatophora: Camaenidae). Molluscan Research 33(2): 130–134. https://doi.org/10.1080/13235818.2013.782794

Páll-Gergely B, Hunyadi A, Hausdorf B (2020) A new species of *Landouria* Godwin-Austen, 1918 (Gastropoda: Stylommatophora: Camaenidae) from Myanmar. The Raffles Bulletin of Zoology 68: 379–386. https://doi.org/10.26107/RBZ-2020-0054

Panha S (1996) A checklist and classification of the terrestrial pulmonate snails of Thailand. Walkerana 8(19): 31–40.

Pfeiffer L (1842) Symbolae ad Historiam Heliceorum. Sectio alterna. T. Fischer, Cassel [Kassel, Germany]. https://doi.org/10.5962/bhl.title.11903

Pfeiffer L (1862) Diagnoses de neuf espèces nouvelles provenant de Siam. Journal de Conchyliologie 10: 39–46. [pl 5 figs 1–7, pl. 6 figs 1–5]

Pholyotha A, Sutcharit C, Panha S (2021a) Rediscovering the dancing semislug genus *Cryptose-melus* Colling, 1902 (Eupulmonata, Ariophantidae) from Thailand with description of two new species. ZooKeys 1076: 43–65. https://doi.org/10.3897/zookeys.1076.75576

Pholyotha A, Sutcharit C, Tongkerd P, Panha S (2021b) Systematic revision of the limestone karts-restricted land snail genus *Aenigmatoconcha* (Eupulmonata: Helicarionidae), with description of a new species. European Journal of Taxonomy 767: 55–82. https://doi.org/10.5852/ejt.2021.767.1487

Pilsbry HA (1934) Zoological results of the Dolan West China Expedition of 1931, Part II, mollusks. Proceedings of the Academy of Natural Sciences of Philadelphia 86: 5–28. [pls 1–6]

Pilsbry HA (1893–1895) Manual of Conchology: Structural and Systematic, with Illustrations of the Species. Second Series: Pulmonata. Volume 9. Helicidae Volume 7. Academy of Natural Sciences of Philadelphia, Philadelphia, xlviii + 366 pp. [71 pls]

Rensch B (1931) Die Molluskenfauna der Kleinen Sunda-Inseln Bali, Lombok, Sumbawa, Flores und Sumba. 2. Zoologisches Jahrbuch, 63, Abt. f. Syst: 1–130.

Rensch B (1934) Zur Kenntnis der Land- und Süßwassermollusken Sumatras. Archiv fur Molluskenkunde, 66: 313–339. [taf. 14]

Schileyko AA (2004) Treatise on recent terrestrial pulmonate molluscs. Part 12. Bradybaenidae, Monadeniidae, Xanthonychidae, Epiphragmophoridae, Helminthoglyptidae, Elonidae, Humboldtianidae, Sphincterochilidae, Cochlicellidae. Ruthenica (Supplement 2): 1627–1764.

Schileyko AA (2011) Check-list of land pulmonate molluscs of Vietnam (Gastropoda: Stylommatophora). Ruthenica 21: 1–68.

Schileyko AA, Kuznetsov AG (1998) Land snails of the genus *Landouria* Godwin-Austen, 1918 and some other Bradybaenidae of Nepal (Gastropoda, Pulmonata). Ruthenica 8: 43–54.

Solem A (1966) Some non-marine mollusks from Thailand, with notes on classification of the Helicarionidae. Spolia Zoologica Musei Hauniensis 24: 1–110. [3 pls]

Sutcharit C, Tongkerd P, Panha S (2017) Land Snails the Invaluable Bio-Resources for the Kingdom of Thailand. The Thailand Research Fund, Bangkok. [In Thai]

Theobald W (1876) Descriptions of some new land and freshwater shells from India and Burmah. Journal of the Asiatic Society of Bengal, Part II 45 (3): 184–189. [pl. 14]

Tumpeesuwan C, Tumpeesuwan S (2019) First verified record of the genus *Landouria* Godwin- Austen, 1918 from Thailand (Gastropoda: Stylommatophora: Camaenidae) with description of a new species. The Raffles Bulletin of Zoology 67: 298–305. https://doi.org/10.26107/rbz-2019-0021

van Benthem Jutting WSS (1950) Systematic studies on the non-marine Mollusca of the Indo-Australian archipelago. II. Critical revision of the Javanese pulmonate landshells of the families Helicarionidae, Pleurodontidae, Fruticicolidae and Streptaxidae. Treubia 20: 381–505.

van Benthem Jutting WSS (1959) Catalogue of the non-marine Mollusca of Sumatra and of its satellite islands. Beaufortia 7: 41–191. [pls 1, 2, map]

Vermeulen JJ, Whitten AJ (1998) Fauna Malesiana. Guide to the Land Snails of Bali. Backhuys Publishers, Leiden.

von Martens E (1860) On the Mollusca of Siam. Proceedings of the Zoological Society of London 28: 6–18.

von Martens E (1867) Die Landschnecken. In: Die Preussische Expedition nach Ost-Asien. Nach amtlichen Quellen. Zoologischer Theil. Vol. 2. Decker, Berlin, 1–447. [22 plates] https://doi.org/10.5962/bhl.title.12726

Zilch A (1966) Die Typen und Typoide des Natur-Museums Senckenberg, 35: Mollusca, Camaenidae (5). Archiv für Molluskenkunde 95: 293–319.